

# STRUCTURE AND FUNCTION OF THE PECTORAL GIRDLE AND FORELIMB OF *STRUTHIOMIMUS ALTUS* (THEROPODA: ORNITHOMIMIDAE)

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**ABSTRACT.** The forelimb and pectoral girdle of *Struthiomimus altus* are described for the first time. The ornithomimid pectoral girdle differs from that of other theropods in having a higher scapular prominence (acromion process), an anterior flange on the supraglenoid buttress, and a narrow, attenuated coracoid.

Osteological and myological comparisons with recent reptiles and birds, combined with muscle scar evidence, suggests that the primary girdle of *Struthiomimus* was oriented somewhat laterally, as in recent crocodiles and lizards, and that it was mobile with respect to the body wall. The potential for extensive protraction and retraction of the humerus is evident, endowing *Struthiomimus* with extensive forereach abilities, combined with limited rotational potential.

In the manus the offset first digit differs from the usual theropod condition in being rotated outwards, away from the midline of the hand. Digits II and III are incipiently coalesced and functioned as a unit. The osteological evidence suggests that the manus of *Struthiomimus* operated as a hooking and clamping structure, rather than as a grasping or raking one.

WHILE the forelimb of ornithomimids is 'coelurosaurian' in length, it lacks the raptorial characteristics of that group, and there has been considerable speculation regarding its function. Osborn (1916) suggested that the first digit was opposable and described the manus as a grasping hand. Later workers, however, have questioned both the opposability of digit I and the grasping ability of the manus (Ostrom 1969; Galton 1971; Osmólska *et al.* 1972).

The forelimb of *Struthiomimus* was figured by Osborn (1916), but only a brief description was given and the scapulocoracoid was not described. The complete forelimb and shoulder girdle are preserved in only a few specimens of North American ornithomimids and in most cases these are either mounted (AMNH 5339, ROM 851) or unprepared (NMC 8632). Consequently most subsequent comparative work has been based on Osborn's incomplete description.

A specimen of *S. altus* with a well-preserved, articulated pectoral limb and shoulder girdle is now available (Nicholls and Russell 1981). We here redescribe the forelimb and describe and figure the scapulocoracoid for the first time. The presence of clear muscle scars on both the humerus and the scapulocoracoid have prompted us to reconsider forelimb function in this species. Inferences drawn with respect to function are based upon Recent comparative material described herein.

Abbreviations used in this work are as follows: AMNH, American Museum of Natural History; BM(NH), British Museum (Natural History); NMC, National Museum of Canada; ROM, Royal Ontario Museum; TMP, Tyrrell Museum of Palaeontology; UA, University of Alberta; UCMZ, University of Calgary, Museum of Zoology; USNM, United States National Museum.

## SYSTEMATIC PALAEOLOGY

Family ORNITHOMIMIDAE Marsh 1890

Genus *Struthiomimus* Osborn 1916 (Emended Russell 1972)

*Struthiomimus altus* (Lambe 1902)

UCMZ(VP)1980.1. Incomplete skeleton consisting of limbs, girdles, gastralia, and fragments of vertebral column and ribs. The specimen was collected from the Judith River Formation (Judithian,

Upper Cretaceous), of southern Alberta, Canada. The left forelimb and pectoral girdle are complete (text-fig. 1) and were found articulated. A description of the specimen and its taxonomic relationships appear elsewhere (Nicholls and Russell 1981).

Little comparative material is available. Scattered podial fragments of ornithomimids are abundant in the bone scrap of the Judith River Formation, but articulated specimens, or even complete elements, are rare. The two best specimens are ROM 851 (*Ornithomimus edmontonicus*) and AMNH 5339 (*S. altus*). ROM 851 is so crushed that few surface details are discernible. Both of these specimens are mounted, making detailed anatomical comparison difficult. They have been described and figured by Parks (1933) and Osborn (1916) respectively. Comparisons of UCMZ(VP)1980.1 with other North American ornithomimids is based primarily on examination of the following specimens: NMC 12441, 8632, 12228, 8902; UA 16182; ROM 851, 840; and also on literature reports.

Russell (1972) defined three genera of North American ornithomimids: *Ornithomimus*, *Struthiomimus*, and *Dromiceiomimus*. We here recognize only the first two, which may be distinguished on the basis of the manus (Nicholls and Russell 1981)—the manus of *Dromiceiomimus* is incompletely known.

#### OSTEOLOGY OF THE PECTORAL GIRDLE AND FORELIMB OF *STRUTHIOMIMUS ALTUS*

##### (a) Orientation

Throughout the subsequent descriptions we have attempted to standardize directional terminology. Due to the difficulty of orienting adult structures in a standard fashion we have chosen to employ developmental terminology and orientation as they relate to the main body and limb axes. In this context all structures have developmental dorsal-ventral, anterior-posterior, and either lateral-medial (limb girdles) or proximal-distal (limbs) axes. All descriptive terminology relates to these axes (refer to orientation arrows on figures for clarification).

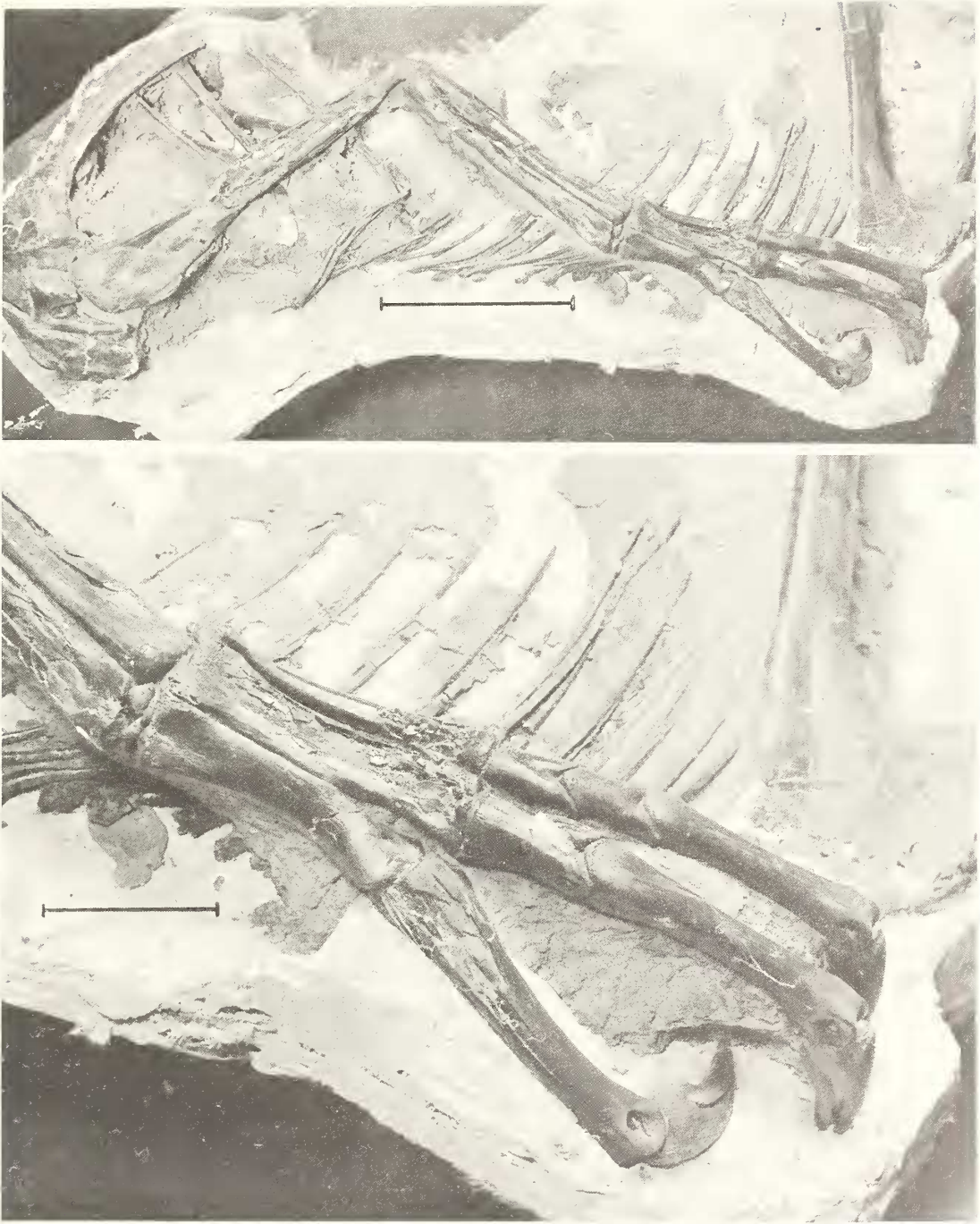
##### (b) Scapulocoracoid

In UCMZ(VP)1980.1 the left scapulocoracoid is complete, except for the dorsal tip of the scapular blade (text-fig. 1). Both coracoids are complete and overlap along the ventral midline. As the left coracoid is partially covered by the right element, the description of the coracoid is a composite, based on the coracoids of both sides. Measurements of the girdle and forelimb are given in Table 1.

The exact length of the scapula is not known, but assuming the scapulo-femoral ratio of UCMZ(VP)1980.1 to be the same as that of AMNH 5339 (Osborn 1916), we estimate the length of the scapula to be 380 mm. It is long and slender and ventrally the shaft is oval in cross-section, but dorsally becomes compressed and blade-like (text-fig. 2) and the shaft has a slight posterior curvature. Although the dorsal tip of the blade is missing, there is no evidence that it was significantly expanded, in accordance with the situation in other ornithomimids.

Situated anteriorly on the scapula, just dorsal to the scapulocoracoid suture, is a compressed, keel-like prominence (text-fig. 2) that has been referred to as the 'acromion process' by several authors (Ostrom 1969, 1978; Osmólska and Roniewicz 1970; Cooper 1981). Its homology with that tuberosity has not been demonstrated, however, and in the absence of clavicles the existence of an acromion can only be surmised. For this reason we have chosen to refer to this structure as the scapular prominence. It is very well developed in *Struthiomimus* (text-fig. 2) as it is also in *Ornithomimus* and *Gallinimus*. It differs, however, from the situation found in most theropods, where the scapular prominence is more pronounced anteriorly but does not extend as far dorsally (text-fig. 3). The anterior edge of the scapular prominence is quite rugose and porous in texture, suggesting the attachment of either muscle or ligament.

The glenoid fossa is deep and sellar. It is equally developed on both scapula and coracoid and has prominent supra- and infraglenoid buttresses. The scapular portion of the glenoid bears an anteriorly directed flange (text-fig. 2), representing an extension of the supraglenoid buttress that resists dorsal deflection of the humerus during extreme humeral protraction.



TEXT-FIG. 1. *a*, the left pectoral girdle and forelimb of *Struthiomimus altus*, UCMZ(VP)1980.1. The scale bar represents 150 mm. *b*, detail of the left manus and wrist. The scale bar represents 50 mm.



TABLE 1. Measurements of the pectoral girdle and forelimb of *Struthiomimus altus* (UCMZ(VP)1980.1).

Scapula—dorsoventral length	380*
—anteroposterior width at midshaft	46
—dorsoventral length of scapular prominence	62
—anteroposterior width of scapulocoracoid suture	88
Coracoid—dorsoventral length, posterior to glenoid	66
—anteroposterior width	179
—length of biceps tubercle	21
—height of biceps tubercle	9
Humerus—proximodistal length	362
—anteroposterior width at midshaft	40
Ulna—proximodistal length	256
—anteroposterior width at midshaft	17
Radius—proximodistal length	239
—anteroposterior width at midshaft	15
Metacarpals, proximodistal length	
—I	102
—II	109
—III	109
Phalanges, proximodistal length	
—I-1	127
—I-2 (ungual)	95
—II-1	40
—II-2	113
—II-3 (ungual)	127*
—III-1	24
—III-2	29
—III-3	89
—III-4 (ungual)	98*
Ungual articular surface dimensions:	Dorsoventral articular height
	Anteroposterior articular width
I-2	21/16
II-3	18/16
III-4	17/15

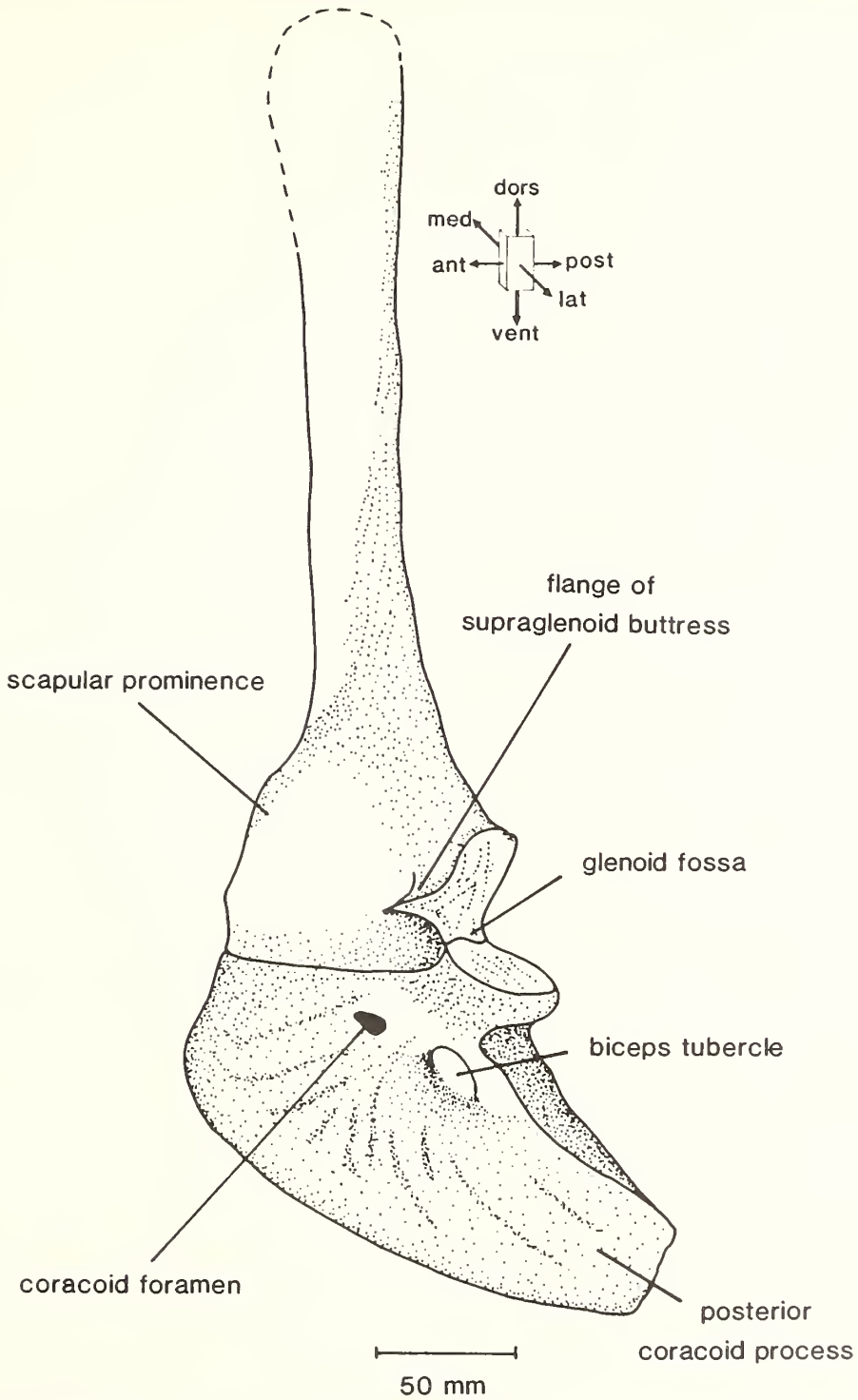
All measurements are in mm, and refer to the left limb and girdle, except for the coracoid which is represented by the right element. Measurements marked with an asterisk (\*) are estimates.

On the dorsal surface of the scapular lip of the glenoid is a narrow, oval depression. A similar depression has been noted in other theropods, notably *Deinocheirus* (Osmólska and Roniewicz 1970) and *Gallimimus* (Osmólska *et al.* 1972) and probably represents the site of origin of the scapular head of the triceps.

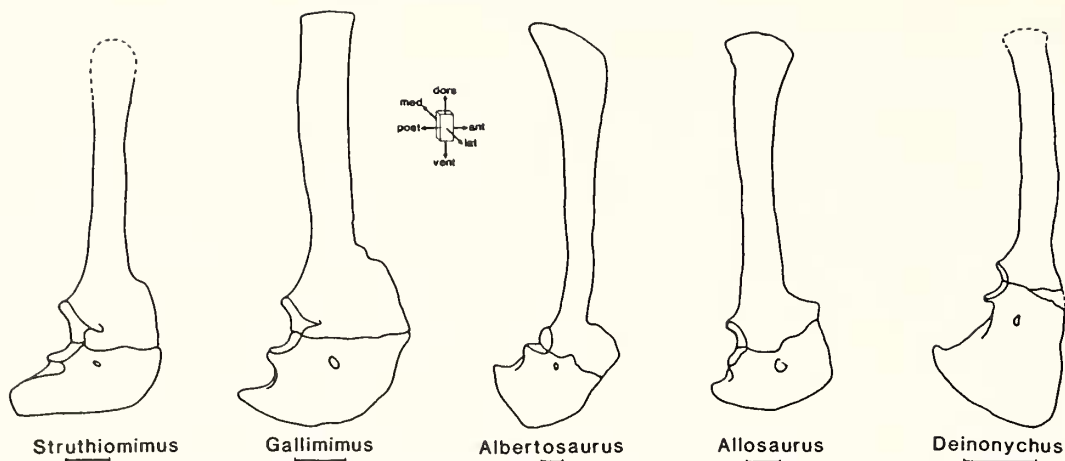
The coracoid is about three times as long as deep, the majority of the length being due to the extension of the posterior coracoid process beyond the glenoid fossa (text-fig. 2). This process does not terminate in a curved apex as it does in most theropods, but is truncated posteriorly. The coracoid is thickest along the dorsal edge of the posterior coracoid process, where it forms a conspicuous infraglenoid buttress.

On the lateral surface of the coracoid plate, ventral to the glenoid, is a pronounced elongate tuberosity, the biceps tubercle (text-fig. 2; Table 1). This corresponds to the 'coracoid tuber' described by Osmólska *et al.* (1972) for *Gallimimus* and to the 'biceps tubercle' of *Deinonychus* (Ostrom 1974)





TEXT-FIG. 2. Left scapulocoracoid of *Struthiomimus altus*, UCMZ(VP)1980.1. Ventromedial curvature removed.



TEXT-FIG. 3. Representative theropod scapulocoracoids compared with that of *Struthiomimus*. All are drawn to approximately the same length for ease of comparison. The scale bar represents 50 mm. In *Struthiomimus* note the narrow, attenuated posterior coracoid process, the anterior flange on the supraglenoid buttress, and the height of the scapular prominence. The latter two characteristics are shared by *Gallimimus*. Diagrams are based on ROM 762 (*Albertosaurus libratus*), ROM 5091 (*Allosaurus fragilis*), and a cast of *Gallimimus bullatus* at the ROM. Data on *Deinonychus* from Ostrom (1974).

and the prosauropod *Massospondylus* (Cooper 1981). It is also well developed in *Dromeosaurus* (TMP 79.20.1) and is present in most long-armed theropods. Ostrom (1974) suggested that the relative size of the biceps tubercle may be related to forelimb length, but this seems unlikely in view of Madsen's (1976) comment that, at least in *Allosaurus*, the development of the biceps tubercle is extremely variable.

There are three clearly defined areas of muscle attachment on the coracoid plate. The most prominent of these is a triangular depression on the dorsal edge of the posterior coracoid process, ventral to the infraglenoid buttress (text-figs. 2 and 11). The depression is very broad and deep, narrows posteriorly, and its surface is quite smooth. This region is interpreted as being the site of origin of the *M. coracobrachialis brevis* (see below).

The other two areas indicative of muscle attachment both lie on the lateral surface of the coracoid plate. The first of these is a broad depression anterior to the glenoid (text-figs. 2 and 11). It overlies the region of the scapulocoracoid suture and the coracoid foramen, extending from the ventral edge of the scapular prominence to the biceps tubercle. This is interpreted as being the site of origin of the *M. supracoracoideus* (see below).

Posterior to the biceps tubercle, the lateral surface of the long posterior coracoid process bears a heavily striated scar (text-figs. 2 and 11), here interpreted as the site of origin of the *M. coracobrachialis longus* (see below). Identical muscle scars were reported by Osmólska *et al.* (1972) for *Gallimimus*.

In overall form the scapulocoracoid of *S. altus* (UCMZ(VP)1980.1) is very like that of the other North American ornithomimids. It does, however, differ considerably from that of other theropods, as noted by Sternberg (1933) in his description of *O. edmontonicus*. In most theropods the depth of the coracoid plate greatly exceeds its length, and the posterior coracoid process is short, terminating in a curved apex ventral to the glenoid (text-fig. 3). A long, shallow coracoid plate with an attenuated coracoid process, an anterior flange extending from the supraglenoid buttress, and a high scapular prominence are all characteristic of the ornithomimid scapulocoracoid. These features are also present in the Mongolian ornithomimids *G. bullatus* (Osmólska *et al.* 1972) and *Archaeornithomimus asiaticus* (USNM 6567, as figured by Gilmore 1933).

*Deinocheirus*, however, sometimes considered to be an ornithomimid (Ostrom 1976a, 1978), has a more typical theropod scapulocoracoid. The scapular prominence is broken in *Deinocheirus*, but appears to extend considerably far dorsally, as in ornithomimids. There is, however, no accessory flange on the supraglenoid buttress and the coracoid is very deep dorsoventrally, and exhibits little extension of the posterior coracoid process.

### (c) Humerus

The left humerus (text-fig. 4) of UCMZ(VP)1980.1 is complete, although the middle of the shaft has been crushed dorsoventrally. It closely resembles the humerus of *Gallimimus* and *Deinocheirus*, although the deltopectoral crest is not as strongly developed as that of the latter genus.

The distal end of the humerus is set at an angle of approximately  $40^\circ$  to the proximal end, a higher degree of torsion than is usual in ornithomimids. In *Gallimimus* this angle is  $25\text{--}30^\circ$  (Osmólska *et al.* 1972) and in NMC 8632, 12441, and ROM 840 it is closer to  $20^\circ$ . Osborn (1916) does not mention the degree of torsion in AMNH 5339 (*S. altus*), although his figures 7 and 8 indicate that some torsion is present. The high degree of torsion in UCMZ(VP)1980.1 may be due to post-mortem deformation, as humeral torsion is also high in ROM 851 ( $35\text{--}40^\circ$ ), which has been crushed in a similar manner.

The anterior tuberosity is fully as high as the head and proximally bears an elongate articular surface that juxtaposes the articular surface of the head (text-fig. 4). This accessory articular surface also encroaches on to the dorsal surface of the humerus and is as well developed as the head. It fits beneath the anterior flange of the glenoid during extreme humeral protraction. Distally, the anterior tuberosity merges gradually with the deltopectoral crest. The latter is poorly developed compared with that of other theropods, its apex being located less than one-fifth of the way along the humeral shaft. It is set at an angle of about  $40^\circ$  to the proximal end of the humerus. On the dorsal surface of the edge of the crest is a thickened lip which possibly marks the separation of the insertion of the *M. pectoralis* and the *M. supracoracoideus*.

Posterior to the deltopectoral crest, on the dorsal surface, a shallow depression extends along the humeral shaft, possibly marking the insertions of the deltoideus musculature.

The posterior tuberosity is only moderately developed. It does not project far out from the shaft, as it does in *Deinonychus* or *Allosaurus*, but extends further along the shaft.

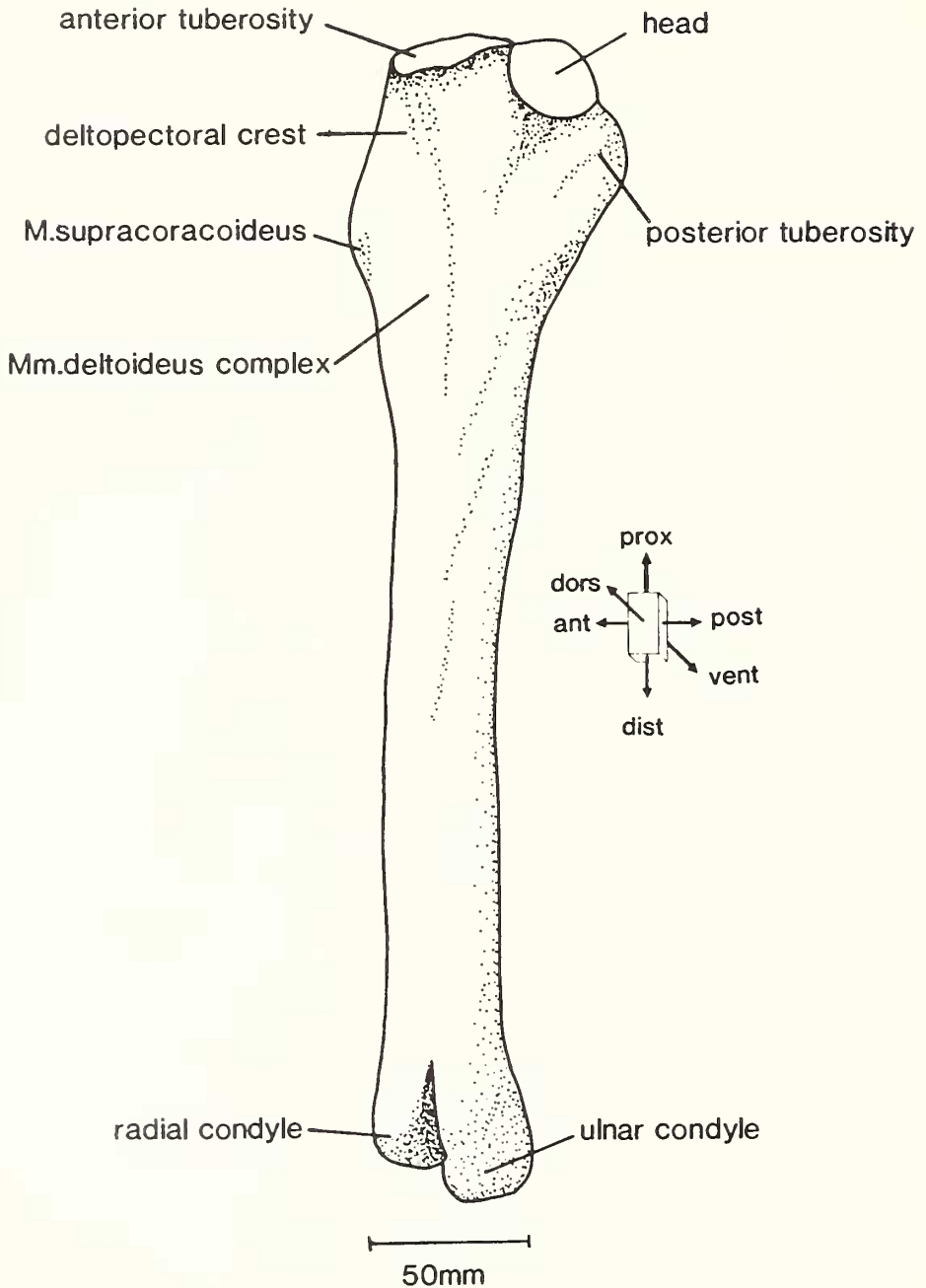
The distal end of the humerus is expanded into a pair of condyles. The ulnar, or posterior, condyle is the larger of the two, extends the furthest distally and is bulbous and symmetrical in plan. The anterior, (radial) condyle is narrow, elongated, and continuous with the ectepicondylar ridge. The two condyles are separated ventrally by a broad fossa. Dorsally the olecranon fossa is present only as a faint depression. The entire distal end of the bone has a rugose, porous surface texture, suggesting the presence of extensive articular cartilage.

### (d) Ulna

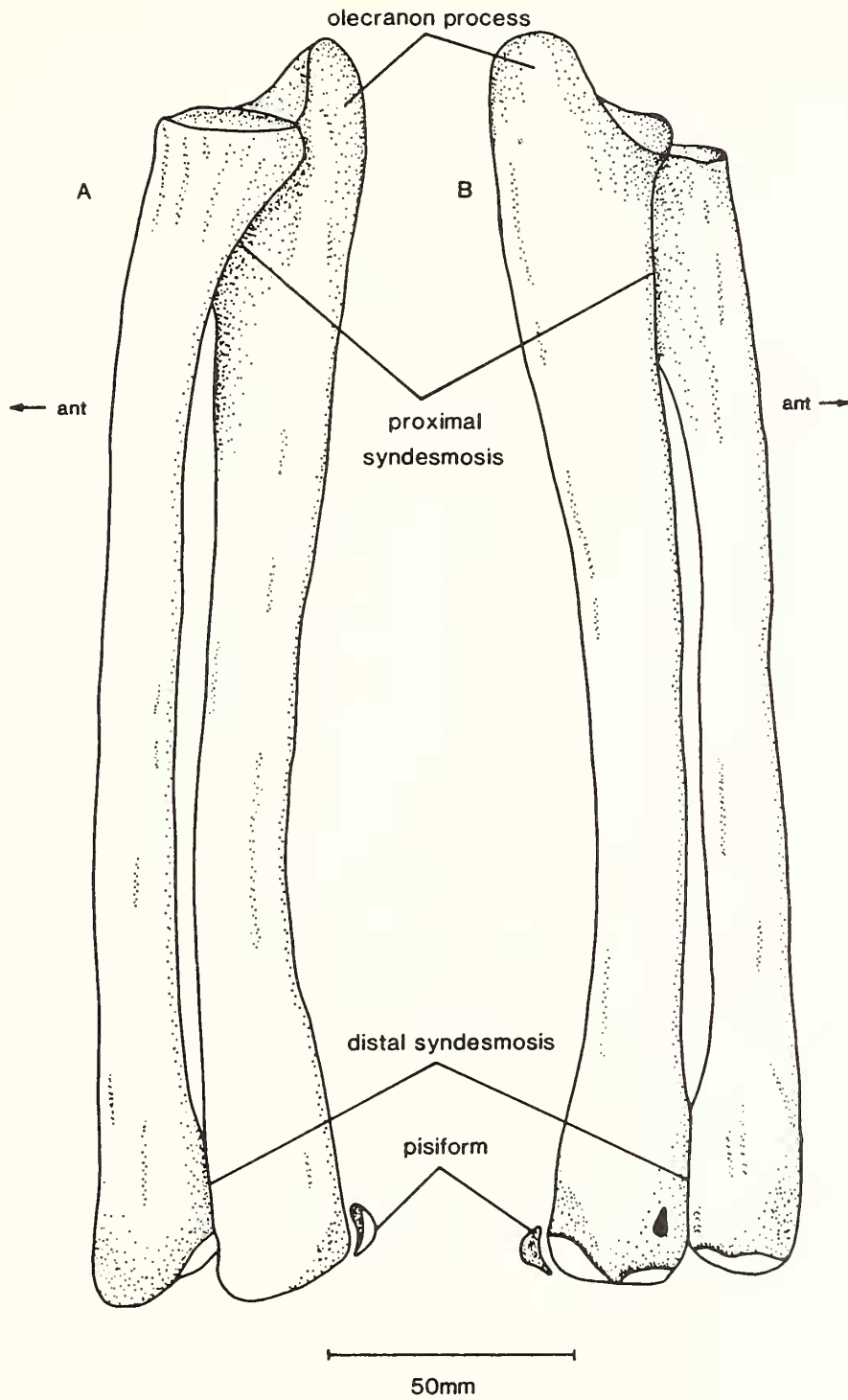
The ulna of UCMZ(VP)1980.1 resembles that of *S. altus*, as figured by Osborn (1916, fig. 8). It is triangular in cross-section and gently curved, being convex toward the radius (text-fig. 5). The olecranon process is long, extending 20 mm proximal to the articular surface of the radius. It is significantly deflected from the ulnar shaft, and manipulation of the osteological preparation at the elbow joint indicates that full extension of the forearm was possible. The concave articular facet for receipt of the radius is deep and well developed. The form of both the proximal and distal radioulnar articulations is suggestive of the presence of syndesmotic unions in life. Such joints, binding the elements by way of collagenous fibres, would permit slight play between the elements but limit rotatory ability.

The distal end of the ulna is crescentic and its anterior edge is flattened along its syndesmotic contact with the radius. On the ventral surface are two condyles separated by a broad, shallow groove (text-fig. 5). The anterior of these is only weakly developed, while the posterior one is larger. A small convexo-concave pisiform is situated adjacent to the posterior condyle. The concave surface of the





TEXT-FIG. 4. Left humerus of *Struthiomimus altus*, UCMZ(VP)1980.1. Dorsal view. M. supracoracoideus and Mm. deltoideus complex refer to the implied insertional areas for these muscles (see text for details).



TEXT-FIG. 5. Radius and ulna of *Struthiomimus altus*, UCMZ(VP)1980.1. A, dorsal view; B, ventral view.

pisiform fits snugly against the posterior ulnar condyle, forming a rotational surface between the ulna and the third metacarpal (text-fig. 6). The entire distal end of the ulna bears numerous striations, suggesting the presence of articular cartilage.

(e) Radius

The radius is almost straight, except at the proximal end where it curves toward the ulna. The proximal articular surface is oval and flat and thus fits perfectly the syndesmotomic articular facet of the ulna, allowing little rotation (text-fig. 5).

Distally the radius is oval in cross-section, except at its contact with the ulna where it is extensively flattened. The distal end of the radius terminates almost 10 mm short of that of the ulna when the two elements are articulated, a point not evident in Osborn's (1916) illustration. This discrepancy in length reflects the form and disposition of the carpals, most of which are concentrated distal to the radius (text-fig. 6).

The distal articular surface of the radius is convex for articulation with the radiale, and the entire distal end of the radius is heavily striated.

(f) Carpus

All of the carpals are excellently preserved, three of them adhering to the distal end of the radius and one to the proximal surface of the metacarpals (text-fig. 6).

The radiale is ovoid in outline, convex distally and concave proximally where it fits the convex surface of the radius. The distal surface of the intermedium is convex and its dorsal outline triangular. The apex of the triangle forms a low ridge which extends along its proximal surface between the radius and ulna. Distally, between the radiale and intermedium, is a small, disc-like bone, probably a centrale. It thins rapidly toward its ventral surface and fits in a slight depression on the proximal end of metacarpal I. The fourth carpal is extremely flattened and closely adherent to the proximal surface of metacarpals I and II. It is so broad and irregularly shaped that it may represent two or more distal carpals in fusion and is here interpreted as distal carpals 2 and 3. The fifth carpal bone is the pisiform, already described under the consideration of the ulna.

Compared with the carpus of other theropods, that of *Struthiomimus* is most like that of *Albertosaurus*, as described by Lambe (1917), although the distal carpals appear to be more specialized. The carpus lacks the well-defined articular facets present in the carpals of *Deinonychus* (Ostrom 1969), and to a lesser extent *Allosaurus* (Madsen 1976). Apparently the carpus of *Struthiomimus* operated as a hinge-joint, permitting little or no rotation, but was not as 'stiff' as indicated by Gregory (in Osborn 1916).

Galton (1971) illustrated six carpals in *Syntarsus* and briefly pared them with the carpals of *Struthiomimus*, although no attempt was made to describe them or to identify the individual elements. The broad, flat anterior distal carpal of *Syntarsus* (Galton 1971, figs. 1 and 3) resembles the fused distal carpals of *Struthiomimus*. The proximal carpals of *Syntarsus*, however, are much flatter than the corresponding elements of *Struthiomimus*, and there is no concentration of the carpals distal to the radius in *Syntarsus*.

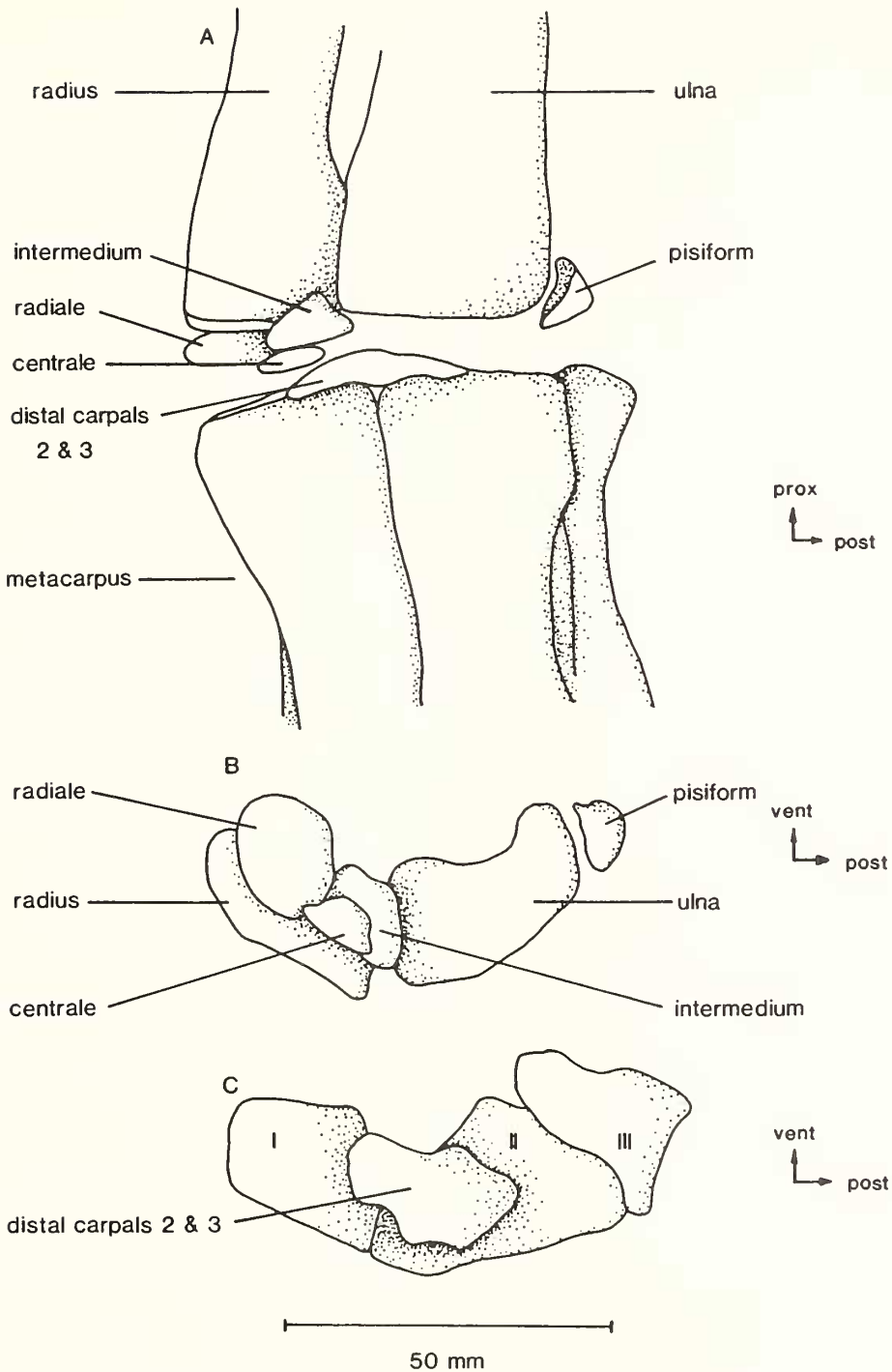
Only one carpal is preserved in *Gallimimus*. This was considered by Osmólska *et al.* (1972) to be the radiale, but it bears no resemblance to any of the carpals of UCMZ(VP)1980.1. In ROM 840 the pisiform and radiale are preserved *in situ* and are like the corresponding bones of *Struthiomimus altus*.

(g) Manus

The manus of UCMZ(VP)1980.1 is very like that of AMNH 5339, as illustrated by Osborn (1916, fig. 3). The three metacarpals are subequal in length, metacarpal I being only slightly shorter than the others. All the metacarpals are tightly adpressed proximally and slightly arched. Distally metacarpal I is strongly divergent and its articular surface is rotated anteriorly.

Two types of joint structure are present in the manus (text-fig. 7). The articulations between the metacarpals and the proximal phalanges are of the ball and socket type, allowing considerable flexion, extension, and rotational movement. The interphalangeal joints, in contrast, are ginglymoid





TEXT-FIG. 6. Carpus of *Struthiomimus altus*, UCMZ(VP)1980.1. A, dorsal view; B, distal view of radius and ulna with attached carpals; C, proximal view of metacarpals with attached carpals. Note, C is represented as a mirror image to keep the alignment for the three parts of the figure constant.

and permit extension and flexion, but little or no rotation, as is usual in the manus of theropods. In the more typically raptorial theropods (e.g. *Ornitholestes*, *Allosaurus*, *Chirostenotes*), groove and keel articulations are present on the metacarpals of both digits I and II. The smoothly rounded distal metacarpal articulation is found on all three digits only in ornithomimids. This type of joint surface permits rotational movement and considerable hyperextension of the digits, but little or no flexion below the horizontal. Most of the flexion in the manus occurred at the interphalangeal joints.

### Digit I

Metacarpal I is closely applied to metacarpal II for a little more than two-thirds of its length, and its posterior edge is flattened along this contact (text-fig. 7). Distally it diverges from the rest of the metacarpus and the distal articular surface is rotated anteriorly and dorsally. Most of the articular surface is smoothly convex. On the dorsal surface, however, there is a deep groove which guides the phalanx anterodorsally (away from the other digits) on extension (text-fig. 7). On flexion, digit I converges on the other two digits. Pits for the collateral ligaments are not as well developed as in Osborn's figure (1916, fig. 3). The pit is moderately developed on the posterior side (which is rotated to face dorsally), but very poorly developed on the anterior side.

The distal articular surface of metacarpal I in *Struthiomimus* differs from that of *Ornithomimus* (ROM 851, NMC 8632), in which metacarpal I is longer and not offset. In *Ornithomimus* the three metacarpals are parallel throughout and their distal articular surfaces are rotated posteriorly. The first metacarpal of *Struthiomimus* more closely resembles that of *Gallimimus*, which is also shortened and rotated anteriorly.

The first phalanx of digit I is the longest phalanx in the manus. Its proximal articular surface is concave and rotated anteriorly. Dorsally there is an enlarged tubercle which fits into the dorsal groove on the distal end of its metacarpal. Distally the grooved articular surface encroaches considerably on to the ventral surface of the phalanx, allowing the ungual to be flexed up to 65–70° below the horizontal. Pits for the collateral ligaments are very deep.

### Digit II

The second metacarpal is flattened anteriorly along its contact with the first. On the proximal articular surface there is a low, broad ventral tubercle. During flexion of the wrist this tubercle fits into the shallow groove between the condyles on the distal end of the ulna (text-fig. 6). Distally the tubercle extends as a stout ridge on the ventral side of the metacarpal.

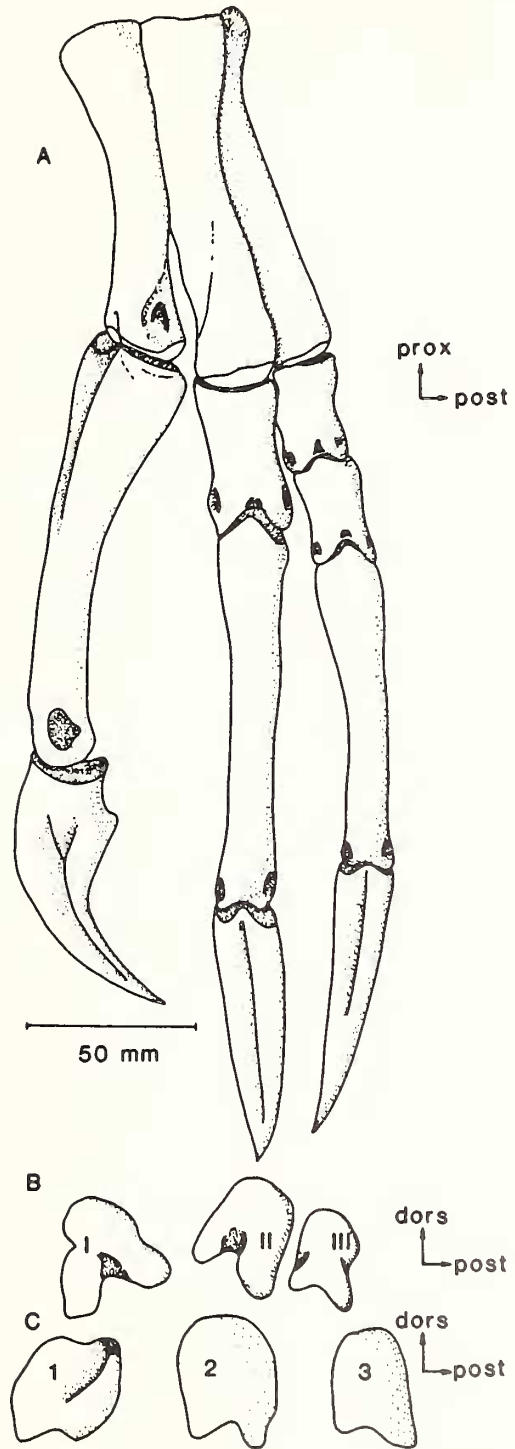
The distal articular surface of metacarpal II lacks any suggestion of the dorsal groove present on metacarpal I. The articular surface is slightly asymmetrical, extending further on the posterior than the anterior side. Pits for the collateral ligaments are only moderately developed.

In the first phalanx the proximal articular surface is smoothly concave, with ventral tubercles for the attachment of the collateral ligaments. The anterior tubercle is much more strongly developed than the posterior one. When articulated with the metacarpal, extension moves the phalanx dorsally and posteriorly away from digit I, and flexion moves it anteriorly and ventrally toward it. The grooved distal articular surface is well developed ventrally, allowing considerable flexion. Pits for collateral ligaments are only moderately developed.

The penultimate phalanx in digit II is very long, being longer than the metacarpal. Pits for the collateral ligaments are well developed and the distal articular surface is of the normal groove and keel type, extending far on to the ventral surface, permitting considerable flexion of the ungual.

### Digit III

The third metacarpal is very slender and is closely adherent to metacarpal II. The distal articular facet is broadly rounded and symmetrically developed. Pits for the collateral ligaments are well developed and open distally, forming a broad groove. On the first phalanx the anterior tubercle for the collateral ligament is more strongly developed than the posterior one, making the proximal articular surface asymmetric in the same manner as the corresponding phalanx in digit II. Extension moves the phalanx posterodorsally.



TEXT-FIG. 7. Manus of *Struthiomimus altus*, UCMZ (VP)1980.1. A, dorsal view of entire manus; B, distal articular surfaces of the three metacarpals in natural position; C, proximal articular surfaces of phalanx I for the three digits. Note, for ease of comparison C is represented as a mirror image so that the alignment of the digits in the three parts of the figure may be kept constant.



The remaining phalanges in digit III all have the normal symmetrical phalangeal ridge and groove articulations. The grooves are very deep and form tightly interlocking joints which permit no lateral displacement. The pits for the collateral ligaments are correspondingly reduced. They are practically non-existent in phalanges 1 and 2, although they are strongly developed in the penultimate phalanx.

### Unguals

In UCMZ(VP)1980.1 the unguis of digit I is complete but the extreme distal tips of unguis II and III have been broken. The unguis are very long and, when covered with a horny sheath during life, must have constituted more than one-third of the length of the manus. The unguis differ from the narrow, highly curved talons of typically raptorial theropods. They are longer, straighter, and broader, being slightly expanded proximally. The articular surface covers the entire proximal end of the unguis and is strongly keeled. The flexor tubercle is not situated directly ventral to the articular surface as in most theropods, but is instead displaced distally about one-quarter of the distance along the phalanx. This greatly enhanced the mechanical advantage of the unguis flexor muscles.

All of the unguis were capable of being highly flexed, forming an angle of almost 70° with the long axis of the penultimate phalanx. The unguis of digit I is the most trenchant of the three, being narrower and more sharply curved than the other two.

The unguis of *Struthiomimus* differ slightly from those of other ornithomimids. Compared to *Ornithomimus*, as defined by Russell (1972), the unguis of *Struthiomimus* are much more robust and more strongly curved. (This, however, may be an allometric feature, as all the specimens identifiable as *Ornithomimus* are smaller animals.) In *Gallimimus* the unguis are shorter and curved, resembling the first unguis of *Struthiomimus*. Osmólska *et al.* (1972) indicated that only a minimal amount of flexion of the unguis was possible in *Gallimimus*, in contrast to the situation in *Struthiomimus* (see above).

Isolated ornithomimid unguis were illustrated and discussed by Ostrom (1969, 1978) in his consideration of the manus of *Deinonychus* and *Compsognathus*. The parameters he used to compare the unguis of theropods were the somewhat equivocal ratio of the length (extension) of the unguis relative to its height, and the angle formed between the cutting edge of the unguis and its arc of rotation. The ornithomimid unguis he used for comparison was that of *O. sedens*, and his figure clearly shows the long, straight, non-raptorial nature of the unguis of *Ornithomimus*. In text-fig. 8 the unguis of UCMZ(VP)1980.1 are compared with those of other theropods. Employing Ostrom's (1969) criteria for claw form and function, the unguis of digit I appears 'subraptorial' and is comparable to those of *Ornitholestes* and *Compsognathus*. The unguis of digits II and III are decidedly non-raptorial.

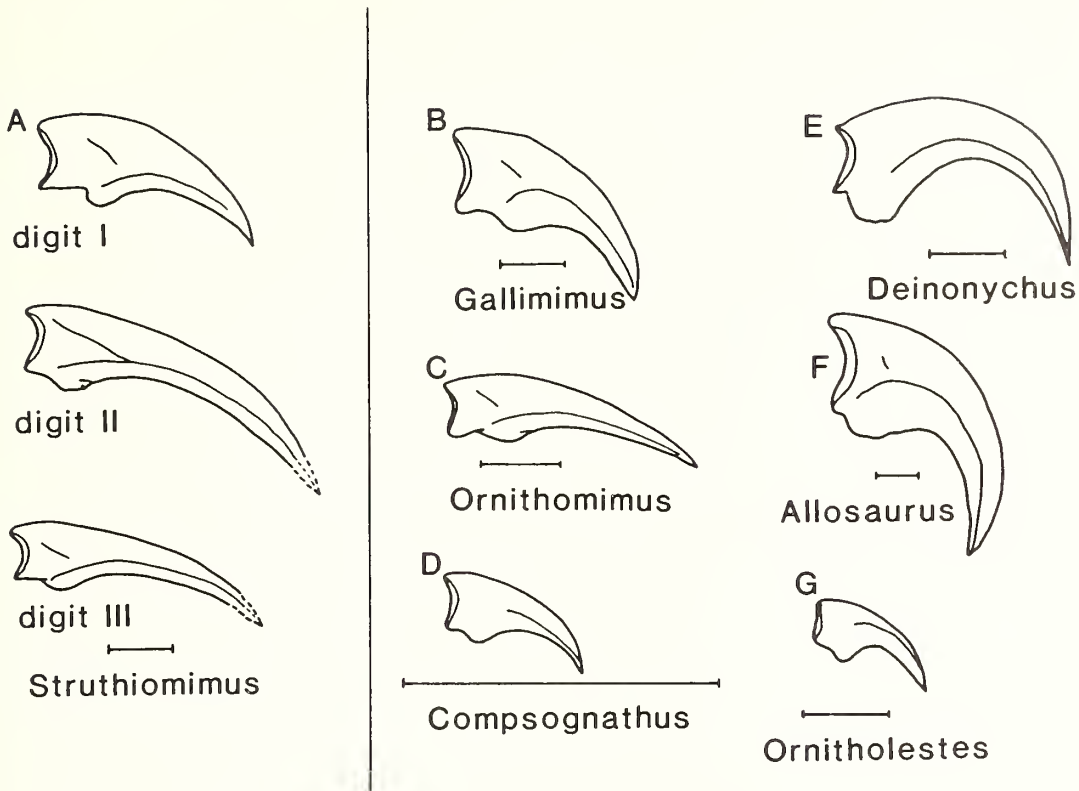
Another parameter useful in comparing unguis is the width of the articular surface, relative to the height, and this is a more reliable criterion for evaluating claw function than the degree of curvature. The true curvature of a claw is formed by its horny sheath, which is seldom preserved in the fossil record. In highly raptorial theropods the unguis are very narrow, with their articular height being almost twice their articular width. As can be seen from Table 1 the unguis of *Struthiomimus* are very broad, their width being almost equal to their height. Again this indicates that they are non-raptorial.

## COMPARATIVE RESULTS—THE BASIS FOR A FUNCTIONAL ASSESSMENT

### (a) Levels of comparison

In order to attempt to gain a mechanically feasible assessment of the form and possible functional attributes of the breast-shoulder apparatus and forelimb of *Struthiomimus*, comparisons of various types were made. Two 'obvious' comparative models come to mind. The first is a comparison with the equivalent structures of crocodylians in an attempt to investigate, as far as possible, similarities due to the existence of homologies (see, for example, Coombs 1978a; Gardiner 1982; Lauder 1981).

In overall body form, however, crocodylians and ornithomimid dinosaurs are relatively dissimilar and, by inference, it seems reasonable to suspect that their way of life was relatively dissimilar also.



TEXT-FIG. 8. The manual unguals of *Struthiomimus altus* compared with those of other theropods. The ungual of digit I is sub-raptorial and comparable with that of *Compsognathus*. The unguals of digits II and III are decidedly non-raptorial. The horizontal scale represents 20 mm. A, *S. altus*, UCMZ(VP)1980.1, digits I, II, and III; B, *Gallimimus bullatus*, cast at ROM; C, *Ornithomimus edmontonicus*, ROM 851; D, *C. longipes*, adapted from Ostrom (1978); E, *Deinonychus antirrhopus*, adapted from Ostrom (1969); F, *Allosaurus fragilis*, ROM 5091; G, *Ornitholestes hermanni*, adapted from Ostrom (1969).

This leads to the second comparison—that with ratite birds. Similarity of form here is not founded upon congruence of homologies but on homoplastic resemblance (similarity due to convergence). This comparison between ornithomimids and ratites can be considered to be somewhat 'classical' in approach, but one in which the basic assumptions have never been tested. The similarity of the ratite pectoral girdle to that of theropod dinosaurs has been most recently discussed by McGowan (1982).

To arrest the comparison at this point, however, and include only *Struthiomimus*, *Alligator*, and *Struthio* cannot fail to produce the expected result—that the breast-shoulder apparatus of the former is structurally and functionally similar to that of *Struthio* due to the great resemblance of form. Such an outcome may or may not be reasonable, but the addition of a third comparison allows a more objective assessment of the resemblances. This third comparison is with chameleons. Chameleons are unusual among normal-limbed lizards in the morphology of their breast-shoulder apparatus and in their mode of progression (Gasc 1963; Peterson 1984). Ostrom (1976a) stated that the narrow form of the scapula found in *Archaeopteryx* occurs only in obligate bipeds (birds, *Archaeopteryx*, and theropod dinosaurs). This is not accurate and, indeed, the primary shoulder girdle of chameleons bears a striking resemblance to that of coelurosaurs, a resemblance that has not gone unnoticed in the

past (Peterson 1973; Bakker 1975). Such similarity, without the influence of potential ancestral-descendant relationships affecting interpretation, forms the basis of the third level of comparison.

(b) Comparative material

The following specimens were dissected (numbers in parentheses refer to number of individuals): *Alligator mississippiensis*\* (1), *Caiman sclerops*\* (1), *Crocodylus niloticus* (BMNH 62.1.24.52) (2), *Struthio camelus*\* (1), *Dromiceius novaehollandiae*\* (2), *Chamaeleo* sp. (3), *Chamaeleo jacksoni*\* (1). Those specimens marked with an asterisk (\*) form part of the University of Calgary Museum of Zoology anatomical collection. Representative skeletal material for all taxa represented was also examined.

(c) The breast-shoulder apparatus: general considerations

In order to be able to more fully appreciate and assess the structural and functional attributes of the breast-shoulder apparatus of *Struthiomimus*, it is necessary to first outline some general points of shoulder structure.

The primary subject of this paper, *Struthiomimus altus*, was apparently an obligate biped. Here the forelimbs and breast-shoulder apparatus have been released from their traditional role in quadrupedal locomotion and exhibit certain features associated with the relative freedom of the limbs. Such differences reflect not only different functions but also different mechanical potentials of the system.

In its most complete (primitive) form the breast-shoulder apparatus consists of paired primary girdles (the scapulocoracoid complexes) of endoskeletal origin, the secondary girdle complex, consisting of paired clavicles and a median unpaired interclavicle, of dermal origin, and an axial endoskeletal component, the sternum (together with its associated ribs). The costosternal complex forms an integral part of the breast-shoulder apparatus. As the primary girdle does not contact the vertebral column, the secondary girdle and costosternal complexes act as a system of braces preventing excessive displacement of the primary girdles but, at the same time, permitting a limited amount of movement with respect to the body wall. The relative structure of the various components, and the nature of the joints between them are, to a large extent, indicative of the functional potentials of the breast-shoulder apparatus (Dvir and Berme 1978).

The release of the forelimb from weight-bearing and its retention as a well-developed structure in an obligately bipedal, non-brachiating form such as *Struthiomimus* has influenced the structure of the breast-shoulder apparatus considerably. The multiple comparisons discussed below attempt to place the form of the apparatus seen in *Struthiomimus* into a biomechanically consistent framework.

(d) Osteological comparative material

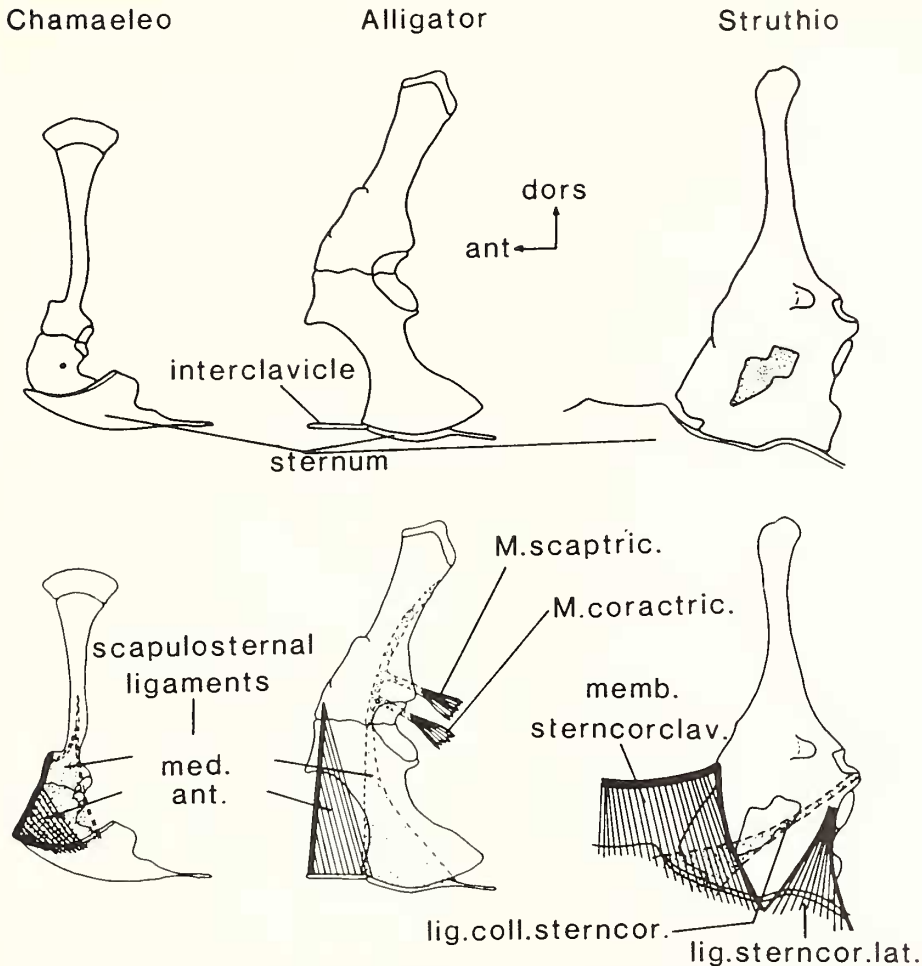
(i) Pectoral girdle of *Alligator* (text-fig. 9)

The breast-shoulder apparatus of crocodylians consists of the scapula, coracoid, interclavicle, and a costosternal system (Kalin 1929). The clavicle is absent and the scapula and coracoid are not fused into a scapulocoracoid plate. The scapula is flattened and blade-like, considerably broader than the scapula of the other forms being discussed, but is only slightly expanded distally. The blade faces laterally and is gently curved to fit the contours of the body wall. The anterior scapular prominence extends well above the level of the glenoid, as in *Struthiomimus*. Posteroventrally the scapula broadens into a stout supraglenoid buttress, on the dorsal lip of which is an oval, roughened area representing the point of origin of the scapular head of the triceps.

The glenoid fossa, to which both the scapula and coracoid contribute equally, is located at the posterior edge of the girdle and faces posterolaterally. The infraglenoid buttress of the coracoid is situated ventral, anterior, and slightly medial to the supraglenoid buttress.

The coracoid is short and deep, its greatest dimension being in the dorsoventral plane. There is no biceps tubercle. The infraglenoid buttress is strongly developed and is situated ventral, anterior, and slightly medial to the supraglenoid buttress. This part of the coracoid plate faces laterally.





TEXT-FIG. 9. Basic form of the primary girdle of the three comparative models discussed in the text. All are viewed from the developmentally lateral aspect regardless of their actual orientation in life. The torsion of the primary girdle of *Struthio* has been artificially removed for ease of presentation. Upper row, primary girdles only; lower row, girdles with major ligament systems superimposed. Ligaments outlined in dashed lines and with their expanse stippled are located on the medial face of the girdle. Each girdle has been drawn to the same dorsoventral linear dimension for ease of comparison. Abbreviations: ant., anterior; lig. coll. sterncor., ligamentum collateralia sternocoracoidea; lig. sterncor. lat., ligamentum sternocoracoideum laterale; M. coractric., M. coracotriceps; M. scaptric., M. scapulo-triceps; med., medial.

Ventral to the glenoid the coracoid curves ventrally and medially to meet the sternum. Posteriorly it forms a small but distinct posterior coracoid process. The ventral edge of the coracoid abuts the lateral edge of the sternum in a frontal plane. The coracosternal angle (the angle the coracosternal articulation makes with the sagittal axis of the sternum) is low.

(ii) Pectoral girdle of *Struthio* (text-fig. 9)

In most birds the forelimb is modified for flight and the morphology of the sternum, coracoid, and limb elements are considerably altered from the 'typical' tetrapod form. In ratites flight has been

secondarily lost (Cracraft 1974), the scapula and coracoid are fused into a single plate and the humerus is less severely rotated.

In *Struthio* the secondary girdle is absent. The pectoral girdle consists only of the scapula and coracoid, fused into a single plate. In this respect the shoulder girdle of *Struthio* resembles that of *Struthiomimus* and other theropods, although no suture is present between the two bones. The distal parts of the forelimb of *Struthio* are much reduced and the shoulder structure is reflective of this. The glenoid fossa is very small relative to the size of the girdle and faces laterally. There is a marked flexure between the scapula and the coracoid, with about 60° of torsion between the plane of the two bones.

Deserving of particular mention is the orientation of the scapulocoracoid plate in life. Whereas in *Alligator* the coracoid is elongated and oriented ventromedially to abut the coracoid sulcus of the sternum, the coracoid of *Struthio*, as is the case in birds in general, has been rotated anteromedially, in association with the reorientation of the coracoid sulcus of the sternum. Here the coracoid abuts the functionally anterodorsal aspect of the sternum and the coracosternal angle is very high. The broad coracoid plate is thus oriented anterolaterally and, as a consequence, the glenoid has come to lie in a much more lateral position. Apart from its torsion the scapulocoracoid plate is essentially planar, the coracoid showing little angulation. The ventral border of the coracoid is straight, not curved, and the posterior coracoid process is reduced.

The coracoid plate is very broad and triangular. There is a large centrally located foramen, but it is not homologous with the coracoid foramen of reptiles and is a derived feature of ratites (Cracraft 1974). Broom (1906) indicated that, developmentally, it is formed by an anterior extension of the scapula ('precapular process') which extends ventrally to join the coracoid at the sternum.

Two distinct tuberosities are present on the scapulocoracoid plate of *Struthio*. The larger of the two was referred to as the 'coracoid tuber' by Cracraft (1974) and was stated to be unique to some ratites. Broom (1906) referred to this tuberosity as the 'acromion process' and McGowan (1982), in his work on the shoulder girdle of kiwis, referred to it as 'the acromial tuberosity'. It is the site of origin of much of the deltoid musculature and it is here referred to as the 'scapular prominence', although its homology with the scapular prominence in other aclaviculate forms has not been demonstrated.

The second tuberosity is situated on the coracoid, ventral and slightly anterior to the glenoid. It is oval in shape with its long axis oriented dorsoventrally. McGowan (1982) calls a similar tuberosity in the kiwi the 'acrocoracoid process'. This structure, by correlation with muscle origins, is the biceps tubercle. It is situated much closer to the glenoid than is the biceps tubercle in *Struthiomimus*.

### (iii) Pectoral girdle of *Chamaeleo* (text-fig. 9)

In outline the pectoral girdle of *Chamaeleo* resembles that of both *Struthio* and theropod dinosaurs. The secondary girdle is absent and the pectoral girdle consists only of a scapula and coracoid, which are fused into a single scapulocoracoid plate. Skinner (1959) reported the transient appearance of clavicles and an interclavicle during chameleontid development, but stated that they disappeared rapidly.

The scapula is a long, thin rod which lacks fenestrae. Ventrally it expands into a scapular prominence anteriorly and the glenoid fossa posteriorly. The scapular prominence is well developed (Siebenrock 1893; Skinner 1959), but does not extend far dorsally, reaching only a little above the level of the supraglenoid buttress. The scapula contributes to a little over one-third of the glenoid fossa and there is a well-developed supraglenoid buttress.

The remaining two-thirds of the glenoid is formed by the unfenestrated coracoid. There is a well-developed infraglenoid buttress which is situated ventral and slightly medial to the supraglenoid buttress. The coracoid is relatively flat, lies in the same plane as the scapula, and faces laterally. The ventral edge is extended posteriorly to form a posterior coracoid process. While this posterior coracoid process is not as well developed as in *Struthiomimus*, it is more prominent than in either *Struthio* or *Alligator* and is comparable to that of many theropods (e.g. *Dromeosaurus* TMP P79.29.1, *Albertosaurus* NMC 2120).

Anterior to, and considerably ventral to, the glenoid is the biceps tubercle. It is in a similar position to the biceps tubercle in *Struthiomimus*, although it is not as prominent as in that genus. It is not at all

like the biceps tubercle of *Struthio*, which is an elongate prominence situated much closer to the glenoid.

The coracoid abuts the anterolateral edge of the sternum *via* a dorsally facing coracoid sulcus. The coracosternal angle is low, being about 30°.

Lecuru (1968*a, b*) distinguished particular features of the lacertilian breast-shoulder apparatus associated with arboreal locomotion, including reduction in the number of scapulocoracoid fenestrae, a tall, narrow scapular blade, modifications of the anteroventral border of the coracoid, and a relatively ventral acromion process (or scapular prominence). Such features reflect adaptation for mobility of the primary girdle on the body wall (Peterson 1973).

(e) Ligament systems of the breast-shoulder apparatus

The ligaments of the breast-shoulder apparatus are seldom considered in studies of the shoulder region, but form an extremely important part of this apparatus when considered as a functional complex. Indeed, consideration of the breast-shoulder apparatus without consideration of the ligament systems means that the functional potential of this apparatus cannot be fully appreciated. Obviously, such systems cannot be reconstructed for fossil forms in any detail, but an appreciation of their architecture in living forms permits some predictive statements to be made.

(i) *Alligator*

In crocodylians a stout anterior scapulosternal ligament is present (text-fig. 9). It arises from the ventral aspect of the scapular prominence and from here fans out as it passes ventrally. Anteriorly it is thickened and forms a stout band which attaches to the anteriormost extremity of the interclavicle. From here it passes posteriorly as a thin sheet which attaches to the interclavicle and the ventral border of the coracoid sulcus of the sternum. It restricts the degree of excursion that can occur at the coracosternal articulation, especially when the humerus is depressed and the limbs become semi-erect. The stout anterior band has the orientation of a clavicle but represents a tensile rather than a compressive structure. Muscular origin from the anterior scapulosternal ligament is meagre.

The medial scapulosternal ligament is continuous with the anterior one on the medial face of the primary girdle. The medial ligament spans the dorsal aspect of the coracosternal articulation and tapers as it passes dorsally across the medial face of the coracoid. At the point where the coracoid curvature is most pronounced it separates from the anterior ligament and attaches to the medial face of the coracoid. From here a slender strand continues dorsally across the coracoscapular joint, passing anterior to the glenoid, and attaches to the medial face of the scapula on its posterior aspect, relatively high up on the shaft. Just dorsal to the glenoid a band of tissue associated with the origin of the *M. scapulotriceps* diverges at right angles from the main course of the ligament, and slightly ventral to this are bands associated with the *M. coracotriceps*.

(ii) *Struthio*

The ligaments of the breast-shoulder apparatus of birds are complex and their nomenclature profuse (see Baumel 1979, pp. 148-151). Essentially, however, the arrangement of ligaments about the coracoid is quite similar to that found in *Alligator*. The furcula, when present, is involved, but the absence of this structure in *Struthio* relieves some of the complication.

Two primary sheets can be recognized. The membrana sternocoracoclavicularis extends from the rostral border of the sternum and crosses the coracosternal articulation to attach to the anterior part of the coracoid and the region of the relatively reduced scapular prominence (text-fig. 9). The membrana sternocoracoclavicularis can be topographically equated with the anterior scapulosternal ligament described for *Alligator* (above). In the case of *Struthio* the interclavicle is absent and the orientation of the coracoid on the sternum is different, but essentially the same topographical points are interconnected. The ligamentum sternocoracoideum laterale of *Struthio* governs the ventrolateral aspect of the coracosternal articulation (text-fig. 9).

The developmentally dorsal lip of the coracoid sulcus of the sternum is spanned by the ligamentum collateralia sternocoracoidea in *Struthio* (text-fig. 9). It passes on to the medial face of the coracoid



for much of its length. There is no association with the *M. scapulo-triceps* and no extension up on to the scapular shaft. The *M. coracotriceps*, generally a vestigial muscle in birds (Berger 1966), is absent in *Struthio* and thus also has no association with the ligamentum collateralia sternocoracoidea.

Topographically the ligamentum collateralia sternocoracoidea of *Struthio* occupies the same basic position as the medial scapulosternal ligament of *Alligator* (above), but morphologically it is more equivalent to the same ligament of *Chamaeleo* (see below). The three ligaments together (membrana sternocoracoclavicularis, ligamentum sternocoracoideum laterale, and ligamentum collateralia sternocoracoidea) govern the mobility at the coracosternal articulation. Mobility of this joint in birds, however, differs from that typically seen in reptiles and the implications of this with respect to coracoid shape and orientation will be more fully considered below.

### (iii) *Chamaeleo*

In *Chamaeleo* the coracoidal arm of the medial scapulosternal ligament of other lizards is absent, permitting greater mobility at the coracosternal articulation (Peterson 1973) (text-fig. 9). There is no connection between the forearm extensor musculature and the medial scapulosternal ligament and the absence of a secondary girdle has, as a correlate, the absence of the mesocleidosternal ligament of other lizards (Peterson 1973).

Among lizards, only in chameleons has an anterior scapulosternal ligament been reported. It is very similar in form to that described for *Alligator* (see above), but no interclavicle is present. The anterior scapulosternal ligament arises from the scapular prominence and passes ventrally along the anterior margin of the scapulocoracoid plate, becomes free of the anterior margin of the girdle, and passes slightly anteroventrally to meet its fellow of the opposite side in the ventral midline. The bilateral ligaments fuse to give rise to a short sagittal ligament which passes posteriorly to attach to the ventral lips of the sternal grooves where they approach each other. Broad bands of fascia connect the transverse and longitudinal arms of the ligament (Peterson 1973).

### (f) Comparative myological material

No attempt has been made to reconstruct all the muscles of the pectoral region of *Struthiomimus*; rather we have restricted our work to those muscles for which there is good evidence in the form of muscle scars. The muscles considered are the following: (i) *M. deltoides scapularis*; (ii) *M. deltoides clavicularis*; (iii) *M. supracoracoideus*; (iv) *M. coracobrachialis*; (v) *M. biceps brachii*; (vi) *M. scapulo-triceps*. Terminology used is that of Romer (1944), unless otherwise noted.

- (i) *M. deltoides scapularis* (text-fig. 10A) (*M. teres major*, Houghton 1867a; *M. dorsalis scapulae*, Fürbringer 1876)

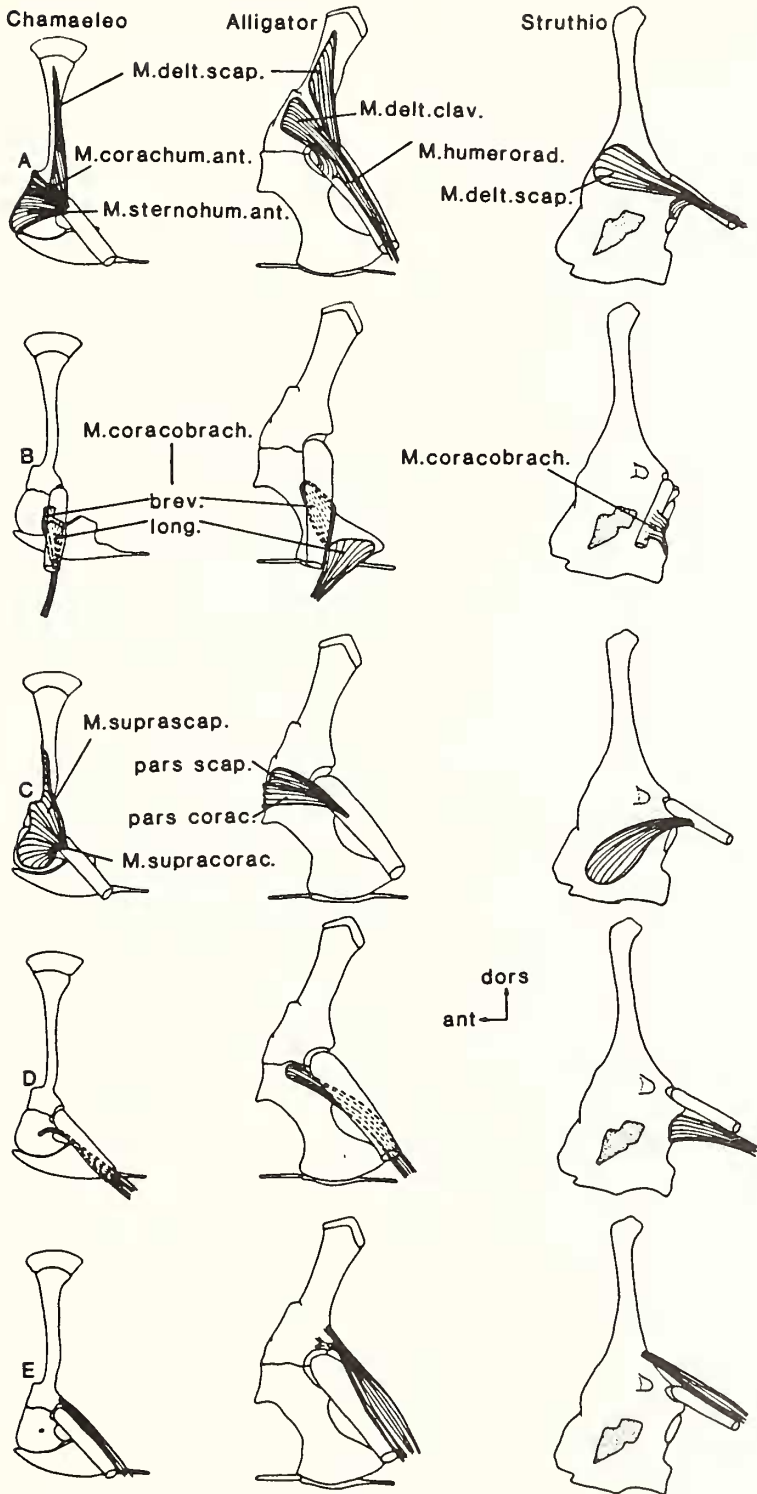
In *Alligator* this muscle arises from the anterolateral surface of the scapular blade. It has a tendinous insertion on the anterodorsal surface of the humerus, just distal of the head.

In *Struthio* the scapulodeltoid (*M. deltoides major*, Berger 1960) arises from the scapular prominence and the anteromedial edge of the scapulocoracoid plate. There is a small secondary head arising from the biceps tubercle. It inserts along the dorsal surface of the humerus, extending more than half way along its shaft. Similar origin and insertion patterns, except for the small accessory

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TEXT-FIG. 10. The form of the muscles discussed for the three comparative models. All are viewed from the (primitively) lateral aspect of the primary girdle. The humerus has been represented in simplified form as a cylindrical rod. A, the *Mm. deltoideus* complex; B, *M. coracobrachialis* with the humerus represented in a protracted and depressed attitude. Dashed portions represent parts of the muscle lying ventral to the humerus; C, *M. supracoracoideus*; D, *M. biceps brachii*. Dashed portions represent parts of the muscle lying ventral to the humerus; E, *M. scapulo-triceps*. Abbreviations: brev., brevis; long., longus; *M. corachum. ant.*, *M. coracohumeralis anterior*; *M. coracobrach.*, *M. coracobrachialis*; *M. delt. clav.*, *M. deltoides clavicularis*; *M. delt. scap.*, *M. deltoides scapularis*; *M. humerorad.*, *M. humeroradialis*; *M. sternohum. ant.*, *M. sternohumeralis anterior*; *M. supracorac.*, *M. supracoracoideus*; *M. suprascap.*, *M. suprascapularis*; *pars corac.*, *pars coracoideus*; *pars scap.*, *pars scapularis*.





head, which appears not to have been reported previously, are described for the emu and rhea by Haughton (1867*b, c*). The accessory head may be the homologue of the *M. deltoideus minor*, caput ventrale of carinate birds (Van den Berge 1979, p. 200).

The absence of an origin of the scapulodeltoid from the scapular blade and the increased insertional length of this muscle are typical avian characteristics (Berger 1960). The origin of this muscle has been brought to lie in a plane which essentially runs along the scapulocoracoid suture and the glenohumeral joint. In so doing its leverage has been altered. Its involvement in humeral elevation is decreased but its part in protraction is enhanced. Its transformation in birds may be associated with the reorientation of the scapulocoracoid and the relative immobility of this element.

In *Chamaeleo* the scapulodeltoid arises from the anterolateral surface of the scapular blade and inserts at the proximal end of the deltopectoral crest of the humerus.

- (ii) *M. deltoideus clavicularis* (text-fig. 10A) (*M. deltoideus scapularis inferior*, Fürbringer 1876; *M. scapulohumeralis anterior*, Romer 1922; Coombs 1978*a*).

None of the forms under consideration have a clavicle. In *Alligator* this muscle arises from the external surface of the scapular prominence, crosses the glenohumeral joint, and inserts on to the dorsal surface of the humerus, medial to the deltopectoral crest. Its insertion interdigitates with the origin of the *M. humeroradialis* (Alix 1874), a developmental derivative of this muscle (Romer 1944).

In birds this muscle is known as the *M. tensor propatagialis brevis* (Van den Berge 1979), or the *Mm. tensores patagii longus et brevis* (Berger 1966). It is absent in *Struthio*, possibly in association with the loss of flight and the reduction of the forelimb and patagium.

In *Chamaeleo* the clavicular deltoid is considerably altered from the usual lacertilian situation and has been subdivided into the *M. coracohumeralis anterior* and the *M. sternohumeralis anterior* (Skinner 1959). Their continuous origin is from the anterior scapulo-sternal ligament, and their insertion is on to the dorsal surface of the deltopectoral crest.

- (iii) *M. coracobrachialis* (text-fig. 10B)

In crocodylians the *M. coracobrachialis longus* is usually considered to be absent (Fürbringer 1876; Romer 1944; Holmes 1977). The most prominent component of the *M. coracobrachialis* (*M. coracobrachialis brevis*, Romer 1944) takes origin from much of the lateral surface of the coracoid plate. It inserts on the proximal ventral surface of the humerus, between the deltopectoral crest and the posterior tuberosity. Dissection of both *Crocodylus* and *Alligator*, however, indicates that this muscle arises by way of two heads—the *M. coracobrachialis brevis* (described above) arising from the broad, external surface of the coracoid plate, and the *M. coracobrachialis longus* having its origin from the posterior coracoid process. The muscle can also be separated into two heads at its insertion on the humerus.

In *Struthio* the single coracobrachialis (*M. coracobrachialis externus*, Romer 1944; *M. coracobrachialis posterior*, Berger 1960; *M. coracobrachialis cranialis*, McGowan 1982) is considered to be homologous, at least in part, to the *M. coracobrachialis brevis* of reptiles (Romer 1944). It arises on the posterolateral edge of the coracoid plate, ventral to the glenoid, and inserts on the ventral surface of the proximal end of the humerus, between the deltopectoral crest and the posterior tuberosity. In *Struthio* it is strongly developed.

The reorientation of the coracoid on the sternum, the reduction of the posterior coracoid process, and the lateral orientation of the glenoid have had a profound influence on the functioning of the *M. coracobrachialis* in *Struthio*. Leverage in humeral retraction is markedly reduced while its role in depression has been enhanced. As in *Chamaeleo* (see below) it has essentially become a part of the glenoid cuff musculature, playing a role in control at the glenohumeral articulation.

In *Chamaeleo* the *M. coracobrachialis longus* arises from the posteolateral surface of the coracoid plate and inserts on the entepicondyle of the humerus. The regression of the posterior coracoid process has reduced its leverage in humeral retraction. The *M. coracobrachialis brevis* arises on the posterior edge of the coracoid, ventral of the glenoid. It inserts on the ventral surface of the humerus, about half-way along the shaft.

(iv) *M. supracoracoideus* (text-fig. 10C)

In *Alligator* the supracoracoideus is divided into two heads. The pars scapularis (Fürbringer 1876) arises on the lateral surface of the scapula, ventral to the scapular prominence. The pars coracoideus (Fürbringer 1876) arises from the medial surface of the coracoid, ventral to the scapular prominence. It curves around the anterior edge of the coracoid to join with the pars scapularis. Together they insert on the deltopectoral crest of the humerus, medial to the insertion of the *M. pectoralis*.

In *Struthio* the *M. supracoracoideus* arises from the broad, anterior surface of the coracoid plate, covering the large coracoid foramen. It soon becomes tendinous, its tendon passing between the scapular prominence and the biceps tubercle. The tendon inserts on the dorsal surface of the humerus, just distal to the head. The importance of the biceps tubercle in supporting the tendon of the *M. supracoracoideus* in birds was noted by Walker (1972) and Ostrom (1976*b*). The particular morphology of the *M. supracoracoideus* in *Struthio* may again be related to the secondary absence of flight capabilities. Its role is in humeral elevation and protraction, but its effectiveness in the former is limited by the relatively ventral position of the biceps tubercle. Similar descriptions of this muscle have been furnished by Haughton (1867*b, c*) for the emu and rhea.

In *Chamaeleo* the supracoracoideus is subdivided into a dorsal *M. suprascapularis* and a ventral *M. supracoracoideus* (Skinner 1959; Peterson 1973). The suprascapularis originates on the anterolateral surface of the scapular ramus, adjacent to the anterior border of the *M. scapulodeltoideus*. The ventral *M. supracoracoideus* takes origin from the anterolateral surface of the coracoid. The two branches have a common insertion at the humeral head, in the plane of the glenohumeral joint.

(v) *M. biceps brachii* (text-fig. 10D)

There is little variation in the biceps in all the forms considered. It arises on the external surface of the coracoid, anteroventral to the glenoid, and inserts on the proximal end of the radius and ulna. In *Struthio* it is considerably reduced in size, probably in association with the reduction in size of the antebrachium. Macalister (1867) reported a separate slip of this muscle arising from the *M. coracobrachialis* in *Struthio*, but we did not locate this, and neither did Haughton (1867*c*) in his examination of the rhea. In *Struthio* and *Chamaeleo* a distinct biceps tubercle is present.

(vi) *M. scapulotriceps* (text-fig. 10E)

In *Alligator* this muscle (*M. anconeus scapulae lateralis externus*, Fürbringer 1876; *M. triceps caput scapularis*, Romer 1922) has a complex origin. It arises by way of three tendons: from the medial surface of the scapula, dorsal to the glenoid; from a branch of the medial scapulosternal ligament; and from the lateral surface of the scapula, at the supraglenoid buttress. It inserts on the olecranon of the ulna.

In both *Struthio* and *Chamaeleo* the *M. scapulotriceps* arises by a single head from the lateral surface of the scapula, dorsal to the glenoid fossa. It inserts on the olecranon process. In *Struthio* it is greatly reduced in size and takes origin considerably further dorsal on the scapula with respect to the glenoid. In *Chamaeleo* origin is close to the glenohumeral joint, but has no connection with the medial scapulosternal ligament. This lack of connection with the ligaments of the breast-shoulder apparatus is a major contributory factor to the enhancement of forereach.

## DISCUSSION

(a) The form and orientation of the primary girdle of *Struthiomimus* in the context of the comparative models

On reviewing the three comparative models, it is immediately apparent that, as expected, there are few overt similarities between the shoulder girdle of *Struthiomimus* and that of *Alligator*. The shoulder girdle of *Alligator* must fulfil the role of both locomotion and support of the animal, and neither of these demands apply to the bipedal *Struthiomimus*.



In comparing the shoulder girdle of *Struthiomimus* with that of *Struthio* and *Chamaeleo*, a number of similarities are apparent. In all three forms the secondary girdle is absent, there is a single scapulocoracoid plate, a long thin scapular blade, and a biceps tubercle.

On closer comparison, however, these similarities in *Struthio* appear to be rather superficial. The scapulocoracoid of *Struthio* consists of a very large coracoid plate but a greatly reduced scapula. This is reflective of the reduced forelimb in the ostrich. The coracoid faces anteriorly and there is about 60° of torsion between the planes of the scapula and the coracoid. The coracosternal articulation is basically a hinge-type structure (Baumel 1979) with a markedly transverse orientation in association with a similar orientation of the coracoid sulci. Manipulation of articulated elements and reports of rhea (Porteilje 1925; Raikow 1969, fig. 3) and ostrich (Sauer and Sauer 1966, figs. 16, 18, and 20) behaviour indicate that the mobility of the forelimbs, important in courtship and aggression, is restricted to the glenohumeral joint and joints distal to this. The ability of the coracoid to slide in the coracoid sulcus is severely limited, and is tightly bound by the ligaments of the breast-shoulder apparatus.

In contrast the scapulocoracoids of both *Struthiomimus* and *Chamaeleo* have well-developed scapulae. There is no torsion and the entire scapulocoracoid faces laterally. Indeed the pectoral girdle of *Chamaeleo* so closely approaches the typical theropod condition that the only obvious difference is that of size. The pectoral girdle of *Chamaeleo*, however, differs markedly from that of terrestrial, sprawling lizards. In terrestrial forms, such as *Iguana*, the secondary girdle is present and the scapulocoracoid is shorter, broader, fenestrated and the coracosternal angle is high. These differences were discussed by Peterson (1971, 1973), who pointed out that the features typical of *Chamaeleo* are associated with the mobility of the scapulocoracoid during arboreal locomotion.

Mobility of the scapulocoracoid plate relative to the sternum plays an important role in the locomotion of many lizards (see Jenkins and Goslow 1983 for an account of locomotion in *Varanus*) but it is particularly well developed in chameleons. The forelimbs of chameleons have been brought closer under the body, in what Bakker (1971) called the 'semi-erect' stance. The absence of a clavicle, the low coracosternal angle, and the modifications of the ligaments of the breast-shoulder apparatus permit the coracoid to slide anteriorly and posteriorly in the coracoid sulcus, concomitantly rotating the girdle in the parasagittal plane. The long scapular blade of chameleons increases the leverage of the muscles that attach dorsally and rotate the girdle. The outcome of girdle rotation in *Chamaeleo* is to increase forereach of the pectoral limb as the animal moves through a discontinuous network of branches (Peterson 1973, 1984).

The relevance to dinosaurs of Peterson's work on chameleonid lizards was recognized by Bakker (1975), but he applied it to quadrupedal dinosaurs. These would incur problems of weight support irrelevant to chameleons because of their small size, and unencountered in bipedal dinosaurs. The biomechanical implications of scapular rotation in quadrupedal dinosaurs were evaluated by Coombs (1978b) and found to be incompatible with the basic morphology of these forms. In *Struthiomimus*, however, the forelimbs are freed from the role of locomotion and weight support.

Considerable mobility also exists in the primary girdle of crocodylians. As in both *Chamaeleo* and *Struthiomimus*, the primary girdle faces laterally and the coracosternal angle is low. At moderate speeds crocodylians exhibit the high walk, essentially a trotting gait (Sukhanov 1968; Whetstone and Whybrow 1983). With increasing speed the high walk gives way to the gallop (Zug 1974; Webb and Gans 1982). Lateral bending in the trunk is not pronounced, this being reflected in the nature of the intervertebral articulations (Hofstetter and Gasc 1969). The intergirdle distance is relatively short (only 15 vertebrae between girdles) and the animals are short-coupled (Peabody 1959). In the relative absence of whole body movements which shift the primary girdle (Daan and Belterman 1968), the rotation of the girdle in the parasagittal plane, with respect to the sternum, performs a similar function.

Thus, the scapulocoracoid plate in crocodylians is mobile in association with speed, while in chameleons it is associated with movement through a discontinuous substrate (Peterson 1984). In both cases, however, the end result is increased forereach.

Another example taken from within the lizards serves to corroborate the utility of the comparisons



based upon *Chamaeleo*. Most geckos are dorsoventrally depressed lizards that exhibit sprawling locomotion with the proximal segments of the limbs held out to the sides of the body (Russell 1975). In one genus, however, there has been a remarkable departure from this typical facies—*Uroplatus* is quite chameleon-like in its habits and overall appearance (Angel 1942). In association with this many of the attributes of the breast–shoulder apparatus of *Chamaeleo* are duplicated or closely approached (Wellborn 1933, pp. 159–160, 193–196, fig. 38). Our interpretation of the breast–shoulder apparatus of *Struthiomimus* indicates similar structural attributes for promoting forereach and forelimb mobility, particularly in the anterior quadrants of the glenohumeral joint.

The problem of orientation of the scapulocoracoid plate on the body wall in theropods has been a persistent one. Ostrom (1974) discussed the scapulocoracoid of *Deinonychus* and proposed an orientation for it similar to that in modern birds, with the scapulocoracoid oriented anteriorly, as in *Struthio*. No consideration, however, was given to the problem of why the coracosternal articulation should be immobile in a form with highly raptorial forelimbs, and it is clear that this would impose severe limitations on forereach. Subsequently, he has represented the scapulocoracoid orientation of *Deinonychus* in both a *Chamaeleo*-like manner (Ostrom 1976c, fig. 2) and an anterior orientation, as in birds (Ostrom 1976a, b). The latter orientation has been disputed by Tarsitano and Hecht (1980).

The long forelimb and well-developed manus of *Struthiomimus* are inconsistent with an immobile, anteriorly oriented scapulocoracoid. Taken over all, and in comparison with recent models, the osteological evidence suggests that the primary girdle of *Struthiomimus* was oriented somewhat laterally, as in *Chamaeleo*, and that considerable excursion was possible with respect to the body wall.

In UCMZ(VP)1980.1 parts of the vertebral column and ribs are preserved. As articulated, the scapular blade curves dorsally and posteriorly, making an angle of approximately 35° with the axis of the preserved vertebrae. The ventral edge of the coracoid plate lies in the same plane as the gastralia and ossified xiphisternal processes (Nicholls and Russell 1981) and this was probably its orientation during life. It is consistent with orientation of the scapulocoracoid in other articulated ornithomimids (ROM 851, NMC 8632, AMNH 5339). In this orientation the medial surface of the scapular blade lies flat against the dorsal ribs and the blade faces laterally. The ventral edge of the scapular prominence curves medially, resulting in an anterior inclination of the scapulocoracoid plate anterior to the glenoid. The glenoid fossa itself faces posterolaterally.

In the region of the scapulocoracoid suture the lateral face of the coracoid plate faces anterolaterally (see above). In the region of the biceps tubercle, however, the coracoid plate curves medially and the external face of the posterior coracoid process faces ventrally while its dorsal edge faces laterally. Consequently the coracoid plate of *Struthiomimus* lies in two distinct planes: anterolaterally, ventral to the scapular prominence and ventrally, in the region of the posterior coracoid process.

The same condition is present in NMC 8632, 8902 and ROM 851, 840. Tarsitano and Hecht (1980), in their discussion of *Archaeopteryx*, state that the coracoid of this genus is more complex than that of other reptiles, in that it lies in two different planes. In fact, the flexure of the coracoid plate that they describe for *Archaeopteryx* is very similar to that present in *Struthiomimus*. Tarsitano and Hecht's statement (1980, p. 163) that the coracoid of theropods 'is a fairly simple plate lying essentially in the same plane as the scapula' is incorrect. Indeed the coracoid of many theropods is curved medially, although not to the extent of that of *Struthiomimus*.

The structure of the sternum in *Chamaeleo* is suggestive of a possible solution for the orientation of the primary girdle in *Struthiomimus*, being compressed, with dorsally turned coracoid sulci. A sternum of this basic type was figured for a specimen of *Albertosaurus* (NMC 2120) by Lambe (1917, figs. 29 and 30). Along the anterior edges of this are notches that appear to represent the coracoid sulci. The curved nature of this sternum (Lambe 1917, fig. 29a) places the sulci in an anterolateral orientation, directed dorsally, quite similar to the situation in *Chamaeleo*. Unfortunately, the restoration of the sternum (Lambe 1917, fig. 30) represents it as a flat plate, artificially placing the coracoid sulci in an anterior orientation, reminiscent of that of birds. That the sternum was a curved or angulated structure is much more likely, however, as only in the former case could the scapular blade take up its orientation against the ribs, as indicated by Lambe (1917, figs. 5, 7, and 49). A similar form for the

sternum of *Massospondylus* is hinted at by Cooper (1981). The coracoid of *Albertosaurus* is discussed by Lambe (1917, p. 47) as being a curved structure. The medial inflection of the coracoid plate would have permitted articulation with the coracoid sulcus, provided a sliding articulation, and placed the scapulocoracoid plate in an appropriate orientation to follow the contour of the body wall. In such an orientation the glenoid would have faced posterolaterally but would have been relatively laterally situated, as in *Chamaeleo*. Orientation of the glenoid into a relatively more lateral situation provides the potential for greater anterior excursion of the forelimb, allowing the humeral head to move more freely into the anterior quadrants of the glenoid.

It is likely, given the structure of the primary girdle and the nature of its ventral coracoid surface, that the sternum of *Struthiomimus* was similar in form to that described for *Albertosaurus* (above). Suggestions that the coracoids of theropods may have overlapped along the midline in life (referred to as arcifery and reminiscent of the pectoral structure in arciferal frogs) (Osmólska and Roniewicz 1970), seem anatomically untenable.

Given this mode of orientation of the scapulocoracoid plate, comparative analysis suggests that the ligament systems of the breast-shoulder apparatus of *Struthiomimus* probably bore most resemblance to those of *Chamaeleo* and *Alligator*. The medial scapulosternal ligament would probably have exhibited the basic form and relationships seen in *Chamaeleo*, permitting freer coracosternal movement and also allowing more degrees of freedom to the mobility of the humeral head. It is also probable that an anterior scapulosternal ligament was present, taking on the form of that seen in *Chamaeleo* and helping to maintain the integrity of the coracosternal articulation during extreme forereach and retraction (Peterson 1973).

(b) Myological reconstruction of the primary girdle of *Struthiomimus*, with reference to humeral mobility

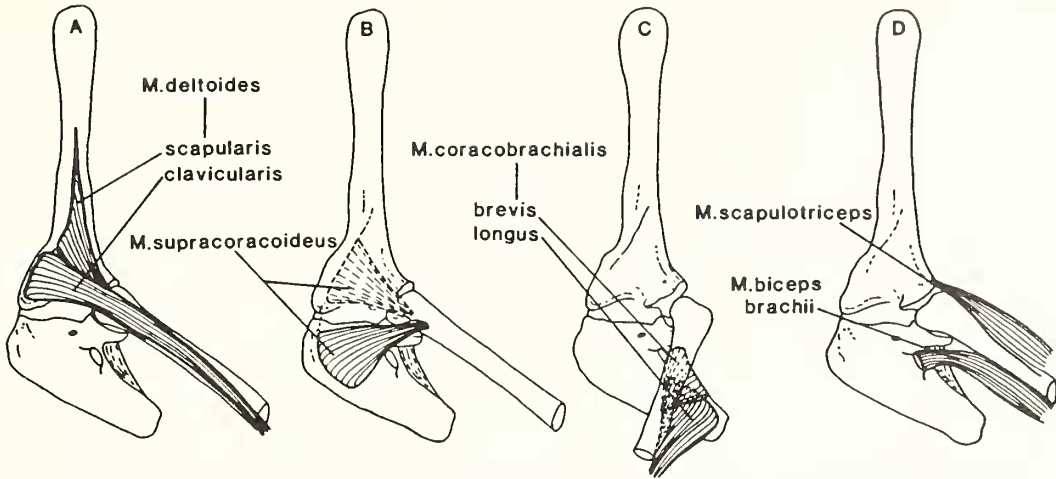
A rather pessimistic view of the utility of muscle scars in muscle reconstruction has been presented by McGowan (1979, 1982). He carried out a detailed study of the musculoskeletal system of the fore and hind limbs of the brown kiwi and stated that it would be impossible to reconstruct musculature from the available osteological data. This view is in general accordance with our own dissections. Only a few muscles were found to leave a discernible scar in *A. mississippiensis* and *Struthio cauehus*. Brown (1981), in his work on the Upper Jurassic Plesiosauroidea, expressed the opinion that there was no osteological evidence for the detailed muscular reconstruction of the plesiosaur humerus as presented by Watson (1924) and Robinson (1975). The question of the propriety of reconstructing the muscles of extinct vertebrates on osteological features is thus raised.

We feel that a compromise probably exists between the views of McGowan and Brown on the one hand and those of other workers who have apparently employed muscle scar evidence to great advantage. Reconstruction of anatomical minutiae seems beyond the scope of muscle scar evidence, but in strongly sculptured regions such as the shoulder, bone architecture is probably a reasonable indicator of at least the major muscles once present in the area. We have restricted ourselves to the attempted reconstruction of major muscles for which good evidence, in the form of scars or major topographical features, seem to exist.

In considering the breast-shoulder apparatus, the location of each muscle in relation to the glenoid and the nature of the muscle belly are important in functional interpretations. The location of muscles with respect to the glenoid will determine the leverage and control over the glenohumeral joint and will influence adduction, abduction, protraction, and retraction. The muscles considered are discussed in the context of the comparative models and their potential actions assessed.

In *Struthiomimus* no distinct muscle scar is present to indicate the point of origin or the *M. deltoides scapularis*. The unreduced nature of the laterally facing scapular blade, however, is reminiscent of the situation in *Chamaeleo* and *Alligator*. It is thus probable that the scapulodeltoid of *Struthiomimus* arose from the anterolateral surface of the scapular blade, as it does in the former two genera (text-figs. 10A, 11A), and promoted extensive humeral protraction and elevation.

Given the carriage of the forelimbs of *Struthiomimus*, their probable involvement in prehension (see below) and their unreduced state, it is unlikely that the *M. deltoides clavicularis* was reduced, as it



TEXT-FIG. 11. Proposed reconstruction of the discussed musculature for *Struthiomimus*. The humerus is represented as a simple cylinder, retracted in A, B, and D, protracted in C. A, the M. deltooides complex; B, the M. supracoracoideus, the dashed portion is an anatomical equivalent to the dorsal portion of this muscle in *Chamaeleo* (see text-fig. 10C), but its presence is conjectural; C, the M. coracobrachialis, dashed portions represent parts of the muscle lying ventral to the humerus; D, the M. biceps brachii and M. scapulotriceps. For further details see text.

is in *Struthio*. The form of the scapular prominence in *Struthiomimus* most closely resembles that of *Alligator* and it is probable that the clavodeltoid arose from the lateral surface of the scapular prominence (text-figs. 10A, 11A). With this configuration the M. deltooides clavicularis would operate primarily as a protractor and elevator of the humerus, and the height of the scapular prominence suggests that these actions were well developed. In comparison with *Chamaeleo* (text-fig. 10A) the M. deltooides clavicularis of *Struthiomimus* appears to be functionally equivalent to the M. coracohumeralis anterior, but not to the M. sternohumeralis which is concerned with humeral protraction in the parasagittal plane.

One of the most prominent features of the coracoid of *Struthiomimus* is the elongate posterior coracoid process. Its lateral surface is heavily striated and there is a deep trough along its dorsal edge. This suggests that the M. coracobrachialis was bipartite. The M. coracobrachialis brevis probably arose from the trough-like depression ventral to the glenoid (text-fig. 11C). This branch would have been most effective in humeral adduction. The M. coracobrachialis longus probably took origin from the lateral face of the extensive posterior coracoid process. Such a posterior origin, relative to the glenoid, suggests powerful humeral retraction and humeral adduction.

Previous considerations of the pectoral myology of dinosaurs (e.g. Ostrom 1974, Borsuk-Bialynicka 1977, Coombs 1978a, Cooper 1981) have generally considered the M. coracobrachialis longus to be absent. This follows Romer's (1944) contention that it is absent in crocodylians. The two heads of the coracobrachialis complex in *Alligator* (text-fig. 10B), and the morphology of the coracoid plate in *Struthiomimus* suggests that the latter bore both branches. As it is closer in its overall orientation to the M. coracobrachialis complex of *Alligator* than *Chamaeleo* or *Struthio* (text-fig. 10B) it is indicative that the humerus could not be elevated greatly above the horizontal plane.

In *Struthiomimus* it is unlikely that the M. supracoracoideus would have been largely tendinous in the region of the glenoid, as it is in *Struthio*. The latter is an avian characteristic and has been much discussed by Ostrom (1976b) and Olson and Feduccia (1979). Ostrom (1976b) associated a prominent biceps tubercle with translating the direction of pull of a ventrally situated M. supracoracoideus, but this need not always be the case, as is evident from *Chamaeleo* (text-figs. 9, 10c).



It is more likely that the supracoracoideus in *Struthiomimus* was a bipartite muscle, as in both *Alligator* and *Chamaeleo* (text-figs. 10C, 11B). The broad depression anterior to the glenoid (text-fig. 2) appears to indicate the origin of the M. supracoracoideus, but this would correspond only to the ventral part of the muscle in *Chamaeleo*. The structure of the glenoid in *Struthiomimus* suggests that the humeral protractors were well developed. Under these circumstances it seems likely that the supracoracoideus would resemble the condition in *Chamaeleo*, extending dorsally along the scapular blade (text-fig. 10C). This would have provided greater versatility of humeral protraction as well as significant elevation. It would have promoted movement of the humeral head into the anterior quadrants of the glenoid, thus enhancing forereach.

The M. biceps brachii of *Struthiomimus* probably arose from the biceps tubercle (text-fig. 11D), inserting on the radius and ulna. The presence of a well-developed antebrachium and manus implies that it would have been a strongly developed muscle, and not a reduced one as in *Struthio*. There is no evidence for a humeral origin of the biceps, as suggested for *Massospondylus* by Cooper (1981).

The anatomical evidence available for *Struthiomimus* suggests that the condition of the M. biceps brachii was intermediate between that of *Chamaeleo* and *Struthio* (text-fig. 10D). Action over the glenohumeral joint would be small and leverage at the elbow strong. It would have been most effective in elbow flexion with the brachium in the forereach position and the humeral head occupying the anterior quadrants of the glenohumeral joint. The closeness of origin to the glenoid would mean that the role of this muscle in protraction would be reduced. The position of the biceps tubercle in *Struthiomimus* may indicate a slightly more medial orientation of the scapulocoracoid plate than is found in *Chamaeleo*.

In *Struthiomimus* a distinct scar is present on the dorsal lip of the supraglenoid buttress close to the glenohumeral joint, that probably represents the point of origin of the M. scapulothoriceps (text-fig. 11D). The morphology of the primary girdle suggests that the M. scapulothoriceps of *Struthiomimus* would have resembled most closely that of *Chamaeleo* (text-fig. 10E). The M. coracothoriceps was probably absent and the humeral head was, therefore, probably endowed with greater degrees of freedom of movement. In summary, the muscles that have been reconstructed by way of comparison with the alligator, ostrich, and chameleon, indicate some particular features of the mobility of the humerus. In *Struthiomimus* the head of the humerus had considerable mobility within the glenoid cavity. The prominent supra- and infraglenoid buttresses of the glenoid and the well-developed anterior and posterior tuberosities of the humeral head suggest that significant degrees of anteroposterior displacement of the humerus, via rotation and translation, were possible, but elevation and depression were much more restricted. Elevation of the humerus could not extend much above the horizontal, but the deltoid complex and the supracoracoideus were developed to bring about powerful elevation to this level, coupled with strong protraction, pulling the humeral head into the anterior quadrants of the glenoid. The biceps was well placed to produce strong flexion of the elbow when the humerus was elevated and protracted. Combined with the mobility of the primary girdle on the sternum (see above), these activities would bring about extensive forereach, resulting in the antebrachium and manus being pushed forward at, or just above, shoulder height, with the potential for the biceps to draw the antebrachium and manus towards the head when the neck was extended.

Acting in an antagonistic fashion the coracobrachialis complex was positioned to bring about powerful humeral retraction and depression, enhanced by the origin arising from the elongate posterior coracoid process. It is unlikely that the M. pectoralis was well developed as the deltopectoral crest is relatively small, compared with that of other theropods, and the angle the crest makes with the proximal articular surface is low. These factors were taken by Ostrom (1969, p. 109) to be indicative of only poorly developed adduction and retraction of the humerus in ornithomimids. It is likely, however, that the coracobrachialis complex assumed a good deal of the responsibility for humeral retraction, but with the humerus in a more horizontal orientation.

In conjunction with this, the scapulothoriceps was positioned to extend the elbow, while the absence of the coracothoriceps would greatly increase the mobility of the primary girdle on the sternum by eliminating one of the chief stabilizing ligaments.



(c) Significance of antebrachial and carpal mobility

The elbow joint of *Struthiomimus* was essentially a hinge joint and the radius and ulna were not freely mobile on each other, but functioned as a unit (see above). Thus, with the humerus elevated and protracted the antebrachium could be flexed and extended to move the manus away from or toward the head.

The concentration of the carpal elements distal to the radius is worthy of comment. That this is their natural position is indicated by the close fit of the proximal ridge of the intermedium between the radius and ulna, and a distinct depression on the proximal end of metacarpal I for reception of the centrale. The same orientation of carpals is seen in AMNH 5339. This concentration of bones proximal to metacarpal I would act like a wedge to displace the metacarpus posteriorly, when the wrist was extended, thus effectively increasing the reach of the first digit.

(d) Functional significance of the manus

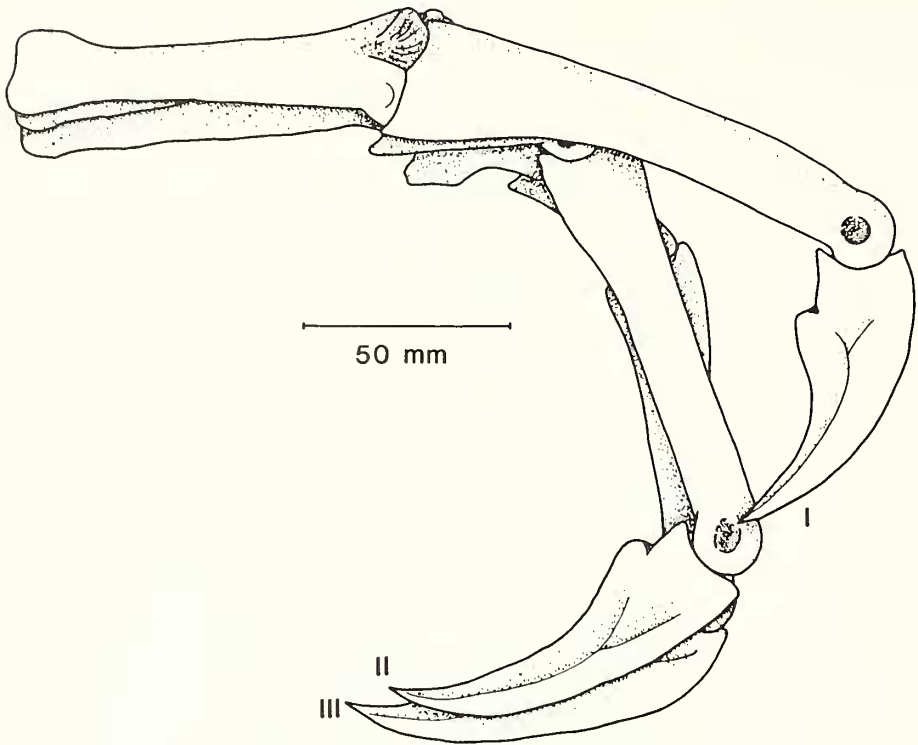
Ostrom (1969) presented a functional analysis of the forelimb of *Deinonychus*, and compared it with that of ornithomimids. He concluded that the forelimb of *Struthiomimus* could not be considered a raptorial grasping structure, as digit I was not truly opposable, the carpus was relatively inflexible and both the internal (our posterior) tuberosity and the deltopectoral crest were poorly developed. Subsequent workers have described the manus of ornithomimids as being relatively weak, and have suggested that the long straight claws were used for lightly raking the surface of the ground to gain access to food (Osmólska *et al.* 1972; Russell 1972). Osmólska *et al.* (1972) have indicated that only very limited flexion was possible in the manus of *Gallimimus*.

We agree with Ostrom that the manus of *Struthiomimus* cannot be considered a grasping or raptorial structure, in the manner of that of *Deinonychus*, but neither can it be considered to be the ineffective, weak structure typical of *Gallimimus* (Osmólska *et al.* 1972). Considerable flexion of all the digits in the manus was possible (text-fig. 12). In a typically raptorial manus, such as that of *Deinonychus* or *Allosaurus*, digits II and III are of unequal length and there is considerable divergence between them. Significant pronation and supination of the manus was also possible, as is evidenced by the articular surfaces of the carpus (at least in *Deinonychus*) and freedom of movement between the radius and ulna. In contrast the forelimb of *Struthiomimus* is characterized by an absence of any significant rotation. The carpus operated as a simple hinge joint and the radius and ulna were firmly syndesmotically united and incapable of independent rotation.

Unique features of the manus of *Struthiomimus* are the nearly equal length of all the digits, the incipient coalescence of digits II and III, and the extreme divergence between digit I and the two lateral digits. The incipient coalescence of digits II and III and their nearly equal length results in these two digits acting in unison. In this regard the manus of *Struthiomimus* resembles that of chameleonid lizards and tree sloths. In chameleons the digits are arranged in opposing sets, while in tree sloths they are in a single set. In both cases, however, the digits are of equal length, are closely applied, and are enclosed in a common sheath of skin that extends to the base of the ungual, holding the digits parallel and causing them to operate as a single unit. Such a sheath may have been present around digits II and III in the manus of *Struthiomimus*.

The divergence of the first digit in *Struthiomimus* has been considered to be a typical theropod characteristic (Ostrom 1969), and Gilmore (1920, p. 61) compared it to that of *Ornitholestes* and *Allosaurus*. While the distal end of the first metacarpal is offset anteriorly in these two genera, as it is in *Struthiomimus*, the nature of the metacarpophalangeal articulation is quite different. In both *Allosaurus* and *Ornitholestes* this articular surface is rotated posteriorly (text-fig. 13). Consequently hyperextension carries digit I dorsally and posteriorly, towards the other digits. When flexed the first digit moves away from the midline of the hand, spreading the digits and broadening the grasp of the raptorial manus.

In *Struthiomimus* the opposite situation exists. The distal articulation of metacarpal I has been rotated anteriorly (text-fig. 13). Hyperextension carries digit I dorsally and anteriorly, resulting in a very wide divergence between digit I and digits II and III. When flexed, digit I moves posteriorly,

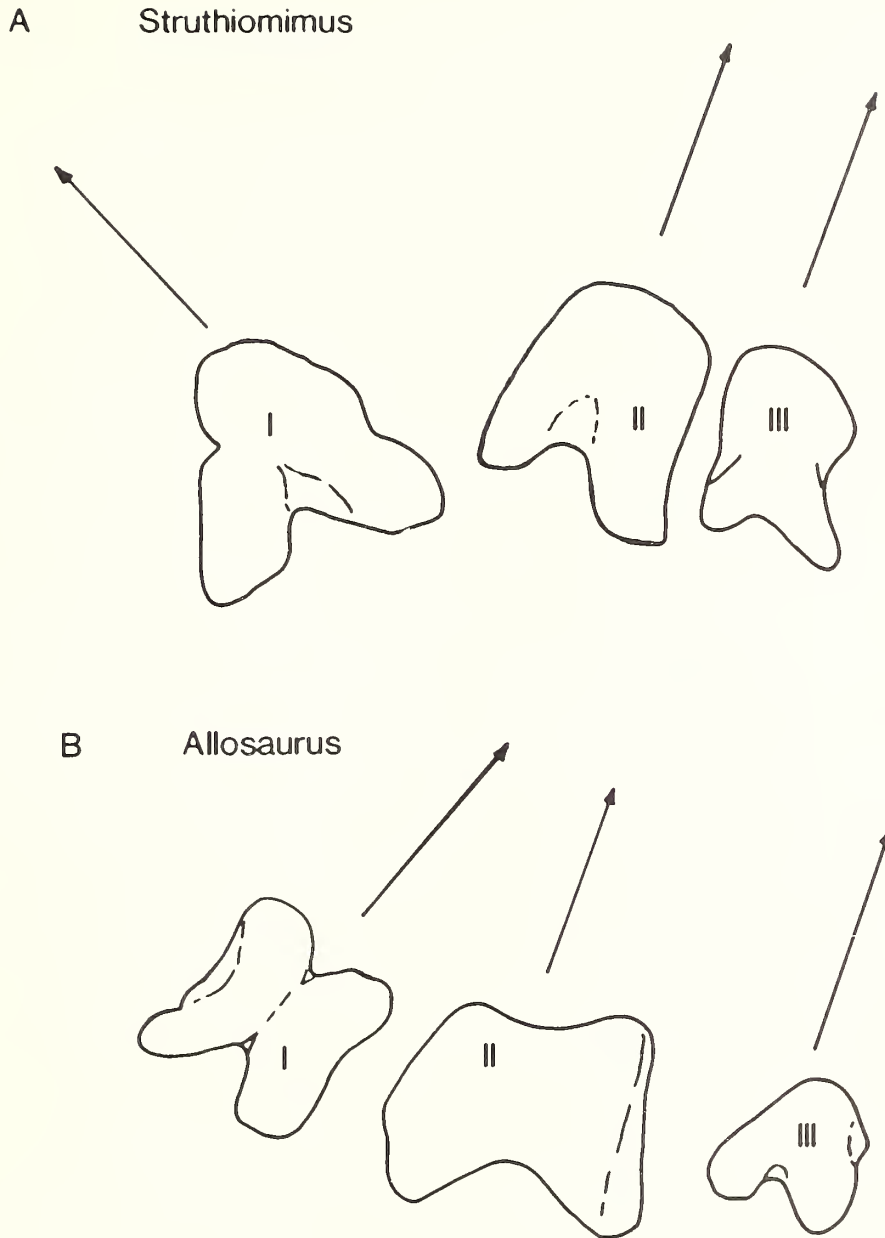


TEXT-FIG. 12. Manus of *Struthiomimus altus* in flexed position, viewed from the anterior aspect.

towards the midline of the hand, effectively narrowing the manus. Flexion also brings digits II and III anteriorly, towards the midline of the hand. With the manus fully flexed the three digits lie close together with digits II and III parallel to one another and digit I converging on these.

The anterior rotation of the distal articular surface of metacarpal I was responsible for Galton's (1971) misinterpretation of Osborn's (1916, fig. 3) figure of the manus of *Struthiomimus*. Galton (1971, pp. 5, 6) suggested that Osborn had incorrectly represented the articular orientation of the first phalanx of digit I, and proposed that instead this phalanx should be rotated clockwise (for the left manus, viewed distally) through  $45^\circ$ . Such a reorientation would result in a more typical theropod configuration of the first digit. Such a reorientation, however, does not accord with the available anatomical evidence. Indeed, Osborn's (1916) interpretation of the orientation of digit I was correct, and the same configuration is evident in UCMZ(VP)1980.1 (text-fig. 1). Rotation of the first phalanx to the position suggested by Galton (1971) results in an anatomically untenable disposition, with the articular surfaces of the first metacarpal and first phalanx not being aligned and, upon extension, the dorsal edge of the first phalanx cutting across the collateral ligament pit on the metacarpal.

Convergence of the digits in flexion is not what would be expected if the manus operated as a raking structure, as has been suggested by Osmólska *et al.* (1972) and Russell (1972). In a rake the prongs are spread to cover a wide area, and a certain amount of digital splay would be expected. Similarly, the manus should be capable of enough pronation to bring the palmar surface parallel to the ground. As has been shown, however, the manus of *Struthiomimus* was capable of little pronation and when fully flexed, the digits of *Struthiomimus* form a very effective hook. The hook-like effect of the manus is enhanced by the elongation of the penultimate phalanx. While this is a characteristic of many theropods, it is particularly well developed in *Struthiomimus*. (The penultimate phalanx makes up



TEXT-FIG. 13. Distal articular surfaces of left metacarpals of *Struthiomimus* compared with those of *Allosaurus*. The arrows indicate the directional path of the first phalanx on hyperextension. In *Struthiomimus* the distal articular surface of metacarpal I has been rotated in a counter-clockwise direction, away from the midline of the hand. Hyperextension results in a very wide divergence between digit I and the remaining digits. In *Allosaurus*, as in most theropods, the distal articular surface of digit I has been rotated in a clockwise direction. When fully extended, the three digits converge. A, *S. altus*, UCMZ(VP)1980.1; B, *A. fragilis*, ROM 5091. (Not drawn to scale.)

29% of the length of digit II on UCMZ(VP)1980.1, compared with 25.6% in *Deinonychus* and 24.6% in *Deinocoelurus*. Data from Ostrom 1969, and Osmólska and Roniewicz 1970, respectively.) In an effective grasping structure the phalanges would be of more uniform length, allowing the digits to curl around their object.

In the elongation of the penultimate phalanx, and in the long, straight unguals, the ornithomimid manus resembles the hook-like manus of tree sloths and anteaters (pers. obs.). The joint structure of the two is different, however. In the edentates there is very little flexion between the short, proximal phalanges, most of the proximal flexion being restricted to the metacarpophalangeal joints (Humphry 1869). In *Struthiomimus* the reverse is true. In both, however, there is considerable potential for flexion of the unguals. The end result is similar—a hook is formed by the elongate unguals. In addition, however, the convergence of the first digit on the second and third in *Struthiomimus*, would also add a clamping function to the manus.

Exactly what *Struthiomimus* was hooking and clamping with its manus can only be surmised. It lacks both the fossorial and the suspensory specialization of living edentates. With their flat, edentulous beaks it is most likely that ornithomimids were herbivorous. Jarzen (1982) has discussed the palynology of the Judith River Formation and indicated that ferns (Polypodiaceae) and tree ferns (Cyatheaceae and Dicksoniaceae) were a significant part of the flora. Cycads were also still abundant. If these were utilized as a food source the hooking action of the ornithomimid manus could be employed to pull fronds, sporangia, or even small branches within reach of its mouth.

#### CONCLUSIONS

The comparative evidence presented has enabled the breast-shoulder apparatus and forelimb of *Struthiomimus* to be reconsidered structurally and functionally. Previous considerations of coelurosaurs and related forms, based chiefly upon avian models, appear to be inadequate. The avian breast-shoulder apparatus exhibits a number of unique specializations associated with the flight mechanism, and these impose several limitations upon the mobility of certain parts of the breast-shoulder apparatus. Extending the comparison to include *Alligator* and *Chamaeleo* has led to the postulation that the primary girdle of *Struthiomimus* was mobile with respect to the body wall and that the forelimb had considerable degrees of freedom of movement.

It is unlikely that the humerus of *Struthiomimus* could have been elevated much above the horizontal, due to the presence of a strong dorsal glenoid buttress, but it could be depressed considerably. The comparative and reconstructed myology, in association with skeletal and ligamentous data, suggest that the forelimb was capable of undergoing considerable protraction with the humerus in the horizontal or semi-vertical position, and that humeral retraction and adduction were relatively powerfully developed. The absence of stabilization of the primary girdle by a secondary girdle and the structural attributes of the forelimb skeleton are consistent with the concept of a highly mobile forelimb. Restriction of primary girdle mobility, as seen in recent birds, is not supported by available morphological evidence.

*S. altus* had elongate forelimbs. In UCMZ(VP)1980.1 the forelimbs are 58% as long as the hindlimbs. Unlike other long-armed coelurosaurs, however, the long forelimbs are decidedly non-raptorial. Rotational movements in the forelimb are limited, there is little digital splay in the manus, and the claws are long and comparatively broad. The major movements of the forelimb appears to have been protraction and retraction at the glenohumeral joint and extension and flexion of the antebrachium and manus.

The manus of *Struthiomimus* was adapted for neither grasping nor raking the ground, as has been previously suggested, but instead appears to have been a specialized clamping and hooking structure. The extreme divergence between digit I and the two lateral digits, when the manus was fully extended, is unequalled in other theropods. The incipient coalescence of digits II and III, and their ability to be strongly flexed suggests that they were enclosed in a common sheath of skin. This hook-like structure of the manus, combined with the extensive forereach of the limb as a whole, suggests that



*Struthiomimus* may have used its long arms for hooking small branches, or the fronds of ferns and cycads, and pulling them within reach of its long neck and edentulous head.

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